EARLY GROWTH, PEST INCIDENCE, AND COLD HARDINESS OF LOBLOLLY PINE, SLASH PINE, AND SOME SLASH PINE HYBRIDS

By

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To my wife, Ma. Eugenia Peña Ortega,

for her love, help, encouragement, and friendship.

To Blanca Elisa and Adriana, my daughters who have changed my life for the better.

To my parents, Fernando y Blanca for their encouragement and love.

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EARLY GROWTH, PEST RESISTANCE, AND COLD HARDINESS OF LOBLOLLY PINE, SLASH PINE AND SOME SLASH PINE HYBRIDS

By

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Chairperson: Timothy L. White
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Eleven field tests with two silvicultural treatments (high intensity and low intensity) were established in the lower Coastal Plains of the southeast USA with seven taxa: (1) improved loblolly pine (PTA); (2) improved slash pine (PEE); (3) unimproved slash pine (PEU); (4) hybrid PEE x PTA; (5) hybrid PEE x *P. caribaea* var. *bahamensis* (PEE x PCB); (6) hybrid PEE x *P. caribaea* var. *hondurensis* (PEE x PCH); and (7) the backcross PEE to PEE x PCH (PEE x F1H). Results at three years of age indicate that PTA was consistently the tallest taxon with the lowest rust incidence but with more tip moth damage in both cultures. The more intensive silvicultural treatment increased height growth and also height differences among taxa on all sites, but 5% more rust incidence was produced. The ratios of infection percentages of PTA and PEE were essentially constant across all sites and in both

silvicultural treatments. Significant genetic gain from breeding for rust resistance was detected at this age for PEE. For height, PEE was 4% and 8% taller than PEU in less intensive and intensive treatments, respectively.

Highly consistent family rankings across sites and across management intensities were detected for rust resistance. Single-site heritabilities ($h^2_{B\,und}$=0.29) were not affected by site or by the increase in management intensity. For height, family rankings were less influenced by environmental differences between treatments than by differences among sites. Stable rankings for height may be expected as cultural intensity increases. More stable family ranking across sites were detected for the high culture than for the low culture. In the high treatment, additive variance was reduced by 6% and environmental error decreased by 25%. This resulted in higher heritability for height in the intensive treatment as compared to less intensive treatment ($h^2_B = 0.3$ *vs.* 0.2, averaged over PTA, PEE and PEU and all sites).

PEE x F1H and PEE x PCB were less affected by cold damage and taller than PEE x PCH, and had height growth similar to the PEE families. All Caribbean x slash hybrids were more susceptible to fusiform rust than PEE. The PEE x PTA hybrid was intermediate for rust incidence and height growth to the PEE and PTA parental species, but mean values were closer to PEE. However, outstanding healthy trees were detected in all hybrid taxa. Larger hybrid heritabilities (h^2_h) and more within-family variability for height compared to within families of parental species were detected and this may be exploited by selection within hybrid families to find outstanding recombinants. PTA and PEE x PTA were the most damaged by tip moth, where *Rhyaciona frustrana* was the most common tip moth species.

CHAPTER 1
INTRODUCTION

In the southeastern United States, substantial areas of land are being withdrawn from forest production to meet other societal needs. Also, forest industry has shifted from harvesting natural forests to growing plantations (Dinus 1974). Further, there is a worldwide emphasis on intensively managing plantations to produce larger volumes per unit of area to satisfy the increasing demand for wood (Hagler 1996).

Loblolly pine (*P. taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelman) are the two most important commercial timber species in the southeastern United States. Appropriate choice between these two tree species may increase wood production through increased growth and resistance to pest damage. Slash pine was widely planted from Virginia to Texas because of its ease of establishment, resistance to tip moth, and verdant appearance (Kellison *et al.* 1979); however, today, loblolly pine has become preferred because of inferior yields of slash from off-site planting and a high mortality rate from fusiform rust (Cole 1975). In the northern portion of the slash pine range (central Georgia), rust incidence is greater on slash than on loblolly pine. However, in the southern portion of loblolly range (northeastern Florida), rust incidence is sometimes greater on loblolly pine (Powers 1975; Kellison *et al.* 1979, Schmidt *et al.* 1985). Powers (1975) stated that the obvious solution is to use both species mainly within their natural range. However, many sites in the lower

Coastal Plain formerly considered appropriate for slash are now planted with loblolly pine (Cole 1975; Kellison *et al.* 1979).

Cultural practices such as site preparation, fertilization, weed control, and pest management have proven effective for increasing the productivity of both loblolly and slash pine plantations in the lower Coastal Plain. However, these practices may alter which species is appropriate for a given site, making the species decision even more complex. No tests have been planted over many sites to examine the effects of operational and intensive management on the more genetically-elite material available from both species.

Hybrids between tree species have been viewed as a method for increasing forest yields. Tree hybrids have fascinated forest geneticists for several decades and many species hybrids have been formed among pines in the southeastern USA. However, in most cases, one or a few parents of each species were used to form the hybrid combinations and the objectives were academic and descriptive (Mergen 1958; Keng and Little 1961; Mergen *et al.* 1965; Saylor and Koenig 1967; Campbell *et al.* 1969; Schmitt 1969; Schmitt and Snyder 1971; Garret 1979). Geneticists have also long been aware that species hybridization has the potential to be a valuable approach to developing genetically-improved, domesticated tree varieties. Among southern pines, the hybrid *P. rigida* Mill. x *P. taeda* L. (grown commercially in Korea) combines the fast growth of loblolly pine with the cold hardiness of pitch pine (Wright 1976). *P. echinata* Mill. x *P. taeda* L. combines the fusiform rust resistance of shortleaf with the faster growth rate of loblolly (Sluder 1970; Kraus 1986).

Several studies have shown that slash pine will cross with loblolly, shortleaf and longleaf pines and that these hybrids have at least some potential value (Derr 1966; Schmitt and Snyder 1971; Wells *et al.* 1978). An analysis of third-year height measurements in Rhodesia showed that there was more within-family variation in the hybrid slash x loblolly pines, than in the non-hybrid families (Barnes and Mullin 1978).

Slash pine (PEE) has also been used to produce hybrids with its subtropical relatives: *P. caribaea* var. *hondurensis* Barret *et* Golfari (PCH) and *P. caribaea* var. *bahamensis* Barret *et* Golfari (PCB) (Nikles 1991; Rockwood and Nikles 1996). One problem of these subtropical pines is their low tolerance to cold temperature. Hybridization with slash pine could improve the resistance to cold (Duncan *et al.* 1996), and perhaps at the same time improve resistance to pest and disease factors. Better growth than slash pine might also result from these hybrids that have evolved in more sub-tropical climates.

The performance of these hybrids has been quite promising elsewhere. In particular, the *P. elliottii* x *P. caribaea* var. *hondurensis* (PEE x PCH) hybrid consistently outperforms pure PEE in environments that are similar to the Lower Coastal Plain of USA. In several South African test sites, the PEE x PCH hybrid averaged 2.5 times as much volume and had better form than pure PEE at 13.5 years of age. Meanwhile, the wood density and pulping characteristics of the hybrids also compared favorably to those of pure PEE (van der Sijde and Roelofsen 1986). In Australia superior growth and generally acceptable wood properties of PEE x PCH favor its use over the pure species in some areas of the subtropics, where parental selection, followed by PEE x PCH evaluation, will ensure wood properties comparable to PEE (Rockwood *et al.* 1991).

Slash pine hybrids have shown tremendous promise in other parts of the world and some are used operationally in Australia (Nikles 1992). PEE x PCH seems promising in southern areas of Florida (Rockwood and Nikles 1996). Also, there has been resurgence of research and testing of hybrids around the world (in many species) as a result of the prospect of efficient systems for mass vegetative propagation of selected hybrid individuals.

Little testing of hybrids has been conducted in the southeastern USA. Thus, in 1994 the Cooperative Forest Genetics Research Program (CFGRP) at the University of Florida undertook a study to investigate the potential of slash pine hybrids in the lower Coastal Plain. Seasonal freezing temperatures may be the most significant factor limiting the potential utility of these hybrids in the southeastern United States, given that the Caribbean pines var. *bahamensis* and var. *hondurensis* occur naturally in frost-free zones and are sensitive to sub-freezing temperatures. However, significant variation in cold resistance has been found among hybrid families (Duncan *et al.* 1996), so the progeny of these hybrids could be used in an advanced improvement program.

A large CFGRP field study was installed to determine the yield potential of four slash pine hybrids compared to pure slash and loblolly pine. In addition, the same series of tests compares improved loblolly pine and improved slash pine and is a realized gains test of improved slash pine compared to unimproved slash pine. Because all taxa may respond quite differently to management intensity, the goal is also to compare their responses to both low and high management intensities, which includes fertilizer, weed control and insecticide application. The seven taxa compared in this study are: 1) slash pine x *P. caribaea* var. *hondurensis* (PEE x PCH); 2) slash pine x the F1 hybrid between slash x *P. caribaea* var. *hondurensis* (PEE x F1H); 3) slash pine x *P. caribaea* var. *bahamensis* (PEE x PCB); 4) slash pine x loblolly pine (PEE x PTA); 5) improved loblolly pine (PTA), 6) improved slash pine (PEE); and 7) unimproved slash pine (PEU).

The purpose of this dissertation project is to evaluate this large experiment at three years of age to quantify results for traits related to early performance such as height growth, cold damage, rust incidence, and tip-moth incidence. These traits were chosen to assess early growth and adaptability, as well as genetic resistance to pests that cause loss in productivity.

In the southeastern USA, fusiform rust is the most important forest tree disease of slash and loblolly pine (Czabator 1971; Anderson *et al.* 1984), and tip moth (*Rhyacionia* spp.) causes severe damage on seedlings or saplings (Berisford 1988). Even though attacks or infections of these pests can occur throughout the life of a pine stand, the most serious damage occurs during the first five years following establishment (Yates 1960; Schmidt *et al.* 1981). Unfortunately, intensive management practices in plantations (including mechanical site preparation, weed control and fertilization) currently used to increase pine growth can also increase the incidence of fusiform rust and tip moth damage (Miller 1977; Burns *et al.* 1980; Burton *et al.* 1985; Hood *et al.* 1988; Shoulders *et al.* 1990). The planting of genetically rust-resistant pines plus other silvicultural manipulations now available have significantly reduced rust incidence in the Southeast (Schmidt *et al.* 1981, 1985; Anderson *et al.* 1984; Powers and Kraus 1986; Powers *et al.* 1993), although findings in fusiform-resistance breeding emphasize the need to constantly broaden the genetic basis of resistance in pine because of the highly variable nature of the pathogen (Powers *et al.* 1981). Almost nothing has been done to determine genetic differences among pine families in resistance to tip moth (Berisford 1988).

Furthermore, many progeny tests are routinely protected by pesticides, and there is no opportunity to identify and select for resistance or to study resistance mechanisms. In fact this procedure could lead to the selection of tree strains that are highly susceptible to the moth (Berisford 1988). Therefore, the examination of taxa and family-within-taxa genetic differences for tip moth and rust resistance is considered a key portion of this study of early adaptation.

The primary goals of this study are to examine the early growth, pest resistance, and cold hardiness of improved loblolly pine, improved and unimproved slash pine and four hybrids planted at 11 field sites in the lower Coastal Plain of the southeastern USA. Because taxa may respond differently to management intensity, hybrid potential and species-site comparisons are studied across two levels of cultural practices (intensive culture and less intensive culture) at each site.

Growth and adaptability are assessed through measurements of survival, height growth, cold damage and pest incidence through three years of age. In particular, rust and tip moth damage are most serious during the first five years, and cold damage is generally more severe in young trees.

In addition to the taxa-level genetic differences described above, this study examines the following within-taxon genetic differences for each of the measures of early growth and adaptability:

1) Family to family differences (there were 16 to 23 families representing each taxon);
2) Within-family variation (i.e., the tree-to-tree within-family variability); and
3) The impact of intensive silviculture on estimates of heritability and genotype by environment interaction for loblolly pine and slash pine.

This dissertation has been divided in four major sections. In Chapter 2, the focus is on the taxa comparison, loblolly *vs*. slash pine, across 11 sites and two management treatments. Also, improved slash pine is compared to unimproved slash pine to estimate realized gains on height growth and rust resistance in relation to site management. The impact of intensive treatment on heritability and genotype x environment interaction (gxe) is investigated in Chapter 3. In Chapter 4, the slash x Caribbean hybrids and PEE x PTA hybrid are compared to pure slash and loblolly pine to examine the adaptation of such hybrids to lower Coastal Plain sites. Growth, cold damage, and rust incidence of the taxa are studied. Possible breeding strategies for those hybrids are discussed. Finally, the Chapter 5 focus is on tip moth damage: the tip-moth incidence in all seven taxa; genetic parameters such as heritability; and possible breeding strategies for tip moth resistance are discussed.

CHAPTER 2
SPECIES DIFFERENCES IN EARLY GROWTH, AND RUST INCIDENCE OF LOBLOLLY AND SLASH PINE

Introduction

Loblolly pine (*P. taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelman) are the two most important commercial timber species in the southeastern United States (Borders and Harrison 1989). Although the natural ranges of loblolly and slash pine overlap, slash pine is generally planted on wet, flat sites, while loblolly pine is planted on the intermediate and upland sites (May 1965; Shoulders and Tiarks 1980; Morris and Campbell 1991).

In the lower Coastal Plain (LCP), studies have shown that loblolly performs as well as or better than slash pine on most sites (Cole 1975; Haines and Gooding 1983), except the very poorly drained flatwoods sites, where comparisons have supported the use of slash pine under conventional, less-intensive silvicultural practices (May 1965; Burns 1973; Kellison *et al.* 1979; Haines and Gooding 1983; Gholz *et al.* 1985). Several studies have examined the response of loblolly and slash pine to cultural practices at levels considered "operational" by forest industries, but few have included intensive silviculture (e.g., Haines and Gooding 1983; Blakeslee *et al.* 1987). Such comparisons are important because of the increasing interest in intensive culture to produce larger volumes of wood (Hagler 1996).

Moreover, there are few instances where genetic improvement has been incorporated into studies with both fertilization and weed control to compare the very best available genotypes of both species (Borders and Harrison 1989; Swindel *et al.* 1988; Neary *et al.* 1990). Fertilization and competition control affect growth and can increase susceptibility to physical damage and pest incidences on trees in both loblolly and slash pine, e.g., fusiform rust, caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* (Blakeslee *et al.* 1987; Miller and Schmidt 1987; Swindel *et al.* 1988; Shoulders *et al.* 1990). Species may respond differently to these challenges.

Studies with plots treated with intensive and less intensive culture provide several opportunities to explore how species respond to silviculture treatments (e.g., Colbert *et al.* 1990), and are also conducive to measuring realized gains from tree improvement programs by including improved and unimproved genotypes from the same species (Dhakal *et al.* 1996).

Using third year data, the primary goals of this chapter are to: (1) Compare the rust incidence and early growth of improved loblolly pine (PTA) and improved slash pine (PEE); and (2) Estimate the realized gains from genetic breeding of slash pine by comparing improved (PEE) vs. unimproved slash (PEU) pine. The two objectives (species-site comparisons and realized gain estimation) are studied across two levels of cultural practices at each of 11 sites in the LCP, because the taxa may respond quite differently to management intensity and site differences.

Materials and Methods

Taxa

This experiment is a subset of a larger series of field experiments established by the Cooperative Forest Genetics Research Program (CFGRP), in which seven different pine taxa are being tested: three slash pine x *P. caribaea* hybrids; the slash x loblolly F1 hybrid, improved slash, unimproved slash pine, and improved loblolly pine (See Chapter 4).

The improved slash taxon (PEE) consisted of open-pollinated seed from 18 slash pine clones which are above average for volume or disease resistance. These parent trees have breeding values ranging from 12 to 40% and from -9 to 53%, with means of 24% and 33% for volume gain and rust resistance (R50), respectively, as predicted by the CFGRP (Appendix A). The volume gains are expressed as percentage gain above unimproved material at 15 years of age. For rust resistance, a lower R50 value indicates more resistance to fusiform rust (White and Hodge 1988; White *et al.* 1988). For example, an R50 of 33% for a given parent indicates that on a given site where unimproved material exhibits 50% rust infection, the progeny of this parent are predicted to have 33% of the trees infected (if the parent tree was mated with males having similar levels of resistance).

The unimproved slash pine (PEU) consisted of open-pollinated seed from 17 parents representative of slash pine as it existed in 1955, before any domestication took place. For comparison, the breeding values of the17 parents for volume ranged from -4 to 13% with a mean of 6% (near 0 as unimproved) and for rust from 45 to 72% with a mean of 58% (near 50% as unimproved).

Since all families are open-pollinated, the average breeding values for the seedlots were calculated considering the breeding values of all clones in the seed orchards where seed was collected and assuming 30% pollen contamination (see Appendix A). In this way, the PEE seedlot was estimated to have a mean of 18.3% for volume gain and an R50 equal to 37.1%. The PEU seedlot was estimated to be 4.9 % for volume gain and 51.3% for rust. When comparing 15-year volume gain of the two taxa, the PEE is expected to have 1.183/1.049 = 12.8% more volume than PEU. Likewise, the rust infection of PEE at any age is predicted to be 37.1/51.3= 0.72 times the infection rate of PEU (Hodge *et al.* 1993a). For example, if PEU has 50% infection, PEE infection is predicted to be 0.72*0.50 = 36%. The improved loblolly (PTA) consisted of open-pollinated seed from17 superior parents mostly from the Atlantic Coastal Plain. Details are not available on breeding values of these parents.

Nursery Phase

Seed of all taxa was collected in 1992. The seeds were cleaned and cold-stored at 5 °C. In early June 1993, seed was disinfected with 10 percent hydrogen peroxide, placed in polybags filled with deionized water, imbibed for 24 hours at 25 °C, and cold stratified at 5 °C for 14 days for PEE and PEU, and 28 days for PTA (Bonner *et al.* 1974). Germination was done under greenhouse conditions, and plants were moved outdoors after transplanting and seedling establishment. Four seedling growers were used to supply the seedlings, and each grower produced the plants for three test sites (Appendix B). Each group of three test locations that shared the same grower is denoted as a series.

No special greenhouse cultural practices were used. The taxa were allowed to grow at different rates in order to permit genetic differences in growth to be expressed. Thus, seedlings were of different sizes at outplanting.

Field Implementation Phase

Eleven field test locations were planted in December 1994 in the lower Coastal Plain, which includes north Florida and the southern portions of Georgia and Alabama (Table 2-1, Appendix B).These sites covered a wide range of soil groups, from well to poorly drained and site indices from 16 to 21 m (base age of 25 years). At each location, the field design consisted of a randomized complete block, nested split-plot design, with three complete blocks, two treatment levels labeled as High (intensive) and Low (less intensive culture), 7 taxa (including the 3 taxa analyzed here: PEE, PEU and PTA), 16 open-pollinated families per taxon and 5 trees per family as a row plot (see Chapter 4 for details).

Within each treatment there were 3 complete blocks and a total of 21 taxon plots (7 taxa x 3 blocks). Each taxon whole-plot within a given treatment level consisted of 80 trees (16 families x 5 trees per family row plot). All together 3360 trees were planted at each site (2 treatments x 3 blocks x 7 taxa x 16 families x 5 trees/family). Tree spacing varied by location from 1.5 x 3.0 m (5x10 ft) to 1.8 x 3.0 m (6x10 ft). A buffer strip of 21 m or more was used to separate the two management treatments to contain the effects of fertilizer and insecticide applications. Also, two to four border rows of treated trees surrounded each treatment plot.

Table 2-1. Field locations of the 11 hybrid studies: name of organization and code, location, site index, rust hazard level, type of soil (CRIFF group) and type of drainage

SITE (Cooperator-Code)	County	Soil	Rainfall (mm)	Rust Hazard	Site Index	Drainage Bedding
Smurfit-Stone Container SSC[1]	Levy Fl	D	1320	Low	19	SP D
The Timber Company TC[1]	Putnam Fl	G	1320	Med	20	MW S
Gilman Paper GIL[1]	Lafayette Fl	C	1350	Med	18	W N
Rayonier RAY[2]	Nassau Fl	C	1320	Low	20	P D
Ga. Forestry Com. GFC[2]	Ware Ga	D	1370	Low	17	SP S
Champion Int. CI[3]	Walton Fl	E	1520	Low	19	MW N
Packaging Corporation of America PCA[3]	Columbia Fl	F	1320	Med	18	MW N
St Joseph L. & D. SJL[3]	Gulf Fl	A	1320	Low	18	P S
Kimberly Clark KC[4]	Escambia Al	A	1600	Low	18	SP N
International Paper IP[4]	Decatur Ga	E	1270	Med	21	W N
Florida Division of Forestry DOF[4]	Santa Rosa Fl	F	1550	Med	16	W N

Seedling growers: SSC 1, RAY 2, CI 3 and, KC 4.

Soil classification and drainage type based on Jokela *et al.* (1991).

Rust hazard based on Anderson and Mistreta (1982), where Low is <20%, Medium is 20-50% of rust incidence.

Site index based on 25 years.

Drainage: SP is somewhat poorly; MW is moderately well; W is well; P is poorly drainage.

Bedding: No is none; S is single; D is double.

Herbaceous weed control was part of the pre-planting site preparation in both cultural treatments across all sites, which included shrubby vegetation removal and chemical applications of Round-up, Arsenal or Accord in both treatments. Chopping, raking and burning were done as needed. On six sites bedding was used, and two sites received double bedding (Table 2-1).

In the low treatment, cultural practices were applied at levels considered operational by forest industries in the southeastern USA. (Table 2-1). No fertilization was used, except for the PCA location where phosphorus was added (in both treatments) at establishment. No weed control was used during the first three growing seasons. Prior to the winter measurement, to facilitate data recording, a glyphosate application was used once in KC (1995) and GIL (1997), chopping in SJL (1996) and mowing in PCA (1997). Also, no insecticide was applied for the control of tip moth (*Rhyacionia* spp.), except for PCA, and one application in GIL during the spring of the second and third year (1996 and 1997).

In the high treatment, fertilizer, weed control and insecticides were applied in 1995, 1996 and 1997 at different rates among sites (Table 2-2). The objective was to create differential growth between management treatments, although specific management regimes varied among sites. Diammonium phosphate (DAP) and potassium chloride (KCl) were used as fertilizers on most sites. Most of the fertilizer applications were made during the spring of the first and second growing seasons. Micronutrients were applied at some sites during the third growing season (Table 2-2). Mowing or spot-sprays of glyphosate were used in the high treatment to control weeds on most sites. Also in the high treatment, insecticide was applied for pine tip moth control. In some locations pest traps were used to determine the

Table 2-2. Treatments applied for the intensively-managed (high) and non-intensively managed (low) blocks at each site location.

Culture	Non-intensively Management (LOW Treatment)	Intensively-Management (HIGH Treatment)
Fertilization:	Establishment: None except 280 kg/ha TSP in SJL.	Establishment: None except 280kg/ha of DAP + 224 kg/ha of KCl in RAY. Year 1: 280kg/ha of DAP + 224 kg/ha of KCl[1] in SSC, TC, GIL, CI, KC and DOF. 224 kg/ha of DAP + 504 kg/ha of KCl in PCA. 336 lb of 10-5-10 in GFC. 224 kg/ha of 10-10-10 +100 kg/ha of S,K,Mg in SJL. Year 2: 16-4-8 + M[2] in DOF. 560 kg/ha of 10-10-10 in IP. 280 kg/ha of DAP in PCA. 336 kg/ha of 10-5-10 in GFC. Year 3: 600 kg/ha of 10-10-10 + M in SSC, RAY, KC, IP and DOF.
Herbicide:	NONE, except Year 1:KC (1x). Year 2: Chopping in SJL (1x). Year 3: GIL (1x). Mowing in PCA (1x).	Year 1: In TC, GIL, GFC and KC (1x). Mowing in DOF. Bush hog in KC (3x). Year 2: GIL, GFC, IP,PCA and KC (1x). Chopping in SJL (1x). Year 3: GIL and DOF (1x). Mowing in PCA (1x)and Bush hog in KC.
Insecticide:	NONE, Except: Year 1: PCA (4x). Year 2: GIL (1x). Year 3: GIL (1x).	Year 1: GIL (1x), KC and IP (2x), SSC and CI (3x),TC and PCA (4x), RAY (5x). Year 2: RAY (6x), IP and KC IP (2x), PCA (4x), DOF (3x). Year 3: GIL (1x), RAY (6x), DOF (2x).

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[1] Elemental application rates of 280 DAP + 224 KCl kg/ha: N=50, P=56, K=112.

[2] Micronutrients, elemental application rates per acre; N=60, P=24, K=50, Ca=20, Mg=10, S=13, Fe=0.5, Zn=0.06, Mn=0.5, Cu=0.06, B=0.06.

Herbicide: Roundup or Atrazine. Insecticide: Asana, sometimes Diomethorate or Pyridine. Application were made at rates: 1x=once, 2x=twice...etc.

timing of insecticide application, which varied from none to six times according to the presence of tip moth damage or the number of moths in the traps.

Sixteen families in each taxon were planted per location, but the families varied slightly among sites. Overall, 18 PEE, 17 PEU and 17 PTA families were represented in these 11 tests, while 11 PEE, 15 PEU and 14 PTA families were common to all sites. The sites in each series (same nursery grower) shared the same 16 families of each taxon.

Variables Measured

The following variables were measured on all 11 sites:

1. Height was assessed at ages 1, 2 and 3 years in the winters of 1995, 1996 and 1997, respectively, and was measured as height of the highest terminal bud.
2. Rust incidence was assessed in the winter of 1997-98 (year 3) and scored as 0 (absence of rust) and 1 (presence of rust, either stem or branch galls); and
3. Survival was assessed at 1, 2 and 3 years of age and scored as a binary trait: 0 (dead) and 1 (alive). This chapter reports the results of the latest measurement at 3 years of age for height and rust incidence.

Statistical Analysis

Data editing and standardization

Data from ten sites were used for height and survival analyses. One site was eliminated from the analyses due to extensive deer damage, resulting in large experimental error for third-year height. For height analysis, an average of 2.5% (range 0 to 8%) of the data points in each block were outliers, distinctly outside the range of measurements. These points were assumed to be either inbred trees or recording errors, and were deleted prior to analysis (Mosteller and Tukey 1977).

For rust and height growth, a graphical analysis was performed to test for homogeneity of error variances by plotting means against MSE obtained from analysis of variance for the data from each treatment (high or low) at each site. The MSEs appeared to be similar across sites and treatments and MSE did not increase as the mean increased and Barlett's test for equality of variance was not significant for either trait. For height growth, both standardized data (by dividing the observations' height by the corresponding square root of MSE -see chapter 3 for more details) and raw data were used for analyses. Since results were similar, the analyses are presented in terms of raw data.

For rust and survival, no standardization to stabilize the variance was performed. Analyses of variance (ANOVA) for each site (single-site analysis) were performed on all the 11 sites. However, for the pooled analyses, using data from nine sites in a single analysis, two sites with less than 15% of the trees infected were not included because low rust incidence levels have inherently small variances (White and Hodge 1987).

Also, for survival and rust incidence, proportions based on plot means were transformed using the arcsine of the square root of percentage (Snedecor and Cochran 1980), but untransformed data were used to obtain the plot means in percentage.

General analysis of variance

To test the main effects (treatments, taxa and interactions), single site analyses were performed based on plot means, i.e., the mean of the data from 5 trees in the same row plot

(Table 2-3). The model used was:

$$Y_{ijkm} = \mu + \alpha_i + b_{j(i)} + \tau_k + \alpha\tau_{ik} + b\tau_{ijk} + f_{m(k)} + \alpha f_{im(k)} + e_{ijkm} \qquad (2\text{-}1)$$

where Y_{ijkm} is the mean of up to 5 trees (if living) in the mth family in the kth taxon in the jth block of the ith treatment,

μ is the population mean,

α_i is the fixed effect for treatment (High *vs.* Low),

$b_{j(i)}$ is the random variable for block within treatment ~ *NID* $(0, \sigma^2_b)$,

τ_k is the fixed effect for taxon (PEE, PEU or PTA),

$\alpha\tau_{ik}$ is the fixed effect for the interaction of treatment by taxon,

$b\tau_{ijk}$ is the random interaction block within treatment by taxon ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$,

$\alpha f_{im(k)}$ is the random interaction treatment by family ~*NID* $(0, \sigma^2_{f\alpha})$,

e_{ijkm} is the error term ~*NID* $(0, \sigma^2_e)$,

where i = 1,2 treatments; j= 1,2,3 blocks; k= 1,2,3 taxa; and m=1,...16 families per taxon.

A second series of ANOVAs was then performed by pooling data across sites and treatments to examine main effects and interactions. These analyses were also based on plot means. The model for the pooled analyses was:

$$Y_{lijkm} = \mu + s_t + \alpha_i + s\alpha_{li} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + b\tau_{ijkt} + f_{m(k)} + sf_{tm(k)} + \alpha f_{im(k)} + s\alpha f_{tim(k)} + e_{tijkm} \qquad (2\text{-}2)$$

Table 2-3. ANOVA for any field location (single-site analysis) showing sources of variation, degrees of freedom (DF) and expected mean squares. Treatments, taxa and their interaction were considered fixed effects, while families, blocks and all interactions with these terms were random.

Source	DF	Expected Mean Square
TREATMENT	1	$\sigma^2_e + c_1\sigma^2_{f\alpha} + c_3\,\sigma^2_{b\tau} + c_5\sigma^2_b + c_6\Sigma\alpha_i^2$
BLOCK (TREAT)	4	$\sigma^2_e + c_3\sigma^2_{b\tau} + c_5\sigma^2_b$
TAXON	2	$\sigma^2_e + c_1\sigma^2_{f\alpha} + c_2\sigma^2_{f(\tau)} + c_3\sigma^2_{b\tau} + c_5\Sigma\tau_k^2$
TREAT*TAXON	2	$\sigma^2_e + c_1\sigma^2_{f\alpha} + c_3\,\sigma^2_{b\tau} + c_4\Sigma\Sigma\alpha\tau_{ik}^2$
BLOCK(TREAT)*TAXON	8	$\sigma^2_e + c_3\sigma^2_{b\tau}$
FAMILY(TAXON)	45	$\sigma^2_e + c_1\sigma^2_{f\alpha} + c_2\sigma^2_{f(\tau)}$
FAMILY(TAXON)* TREAT	45	$\sigma^2_e + c_1\sigma^2_{f\alpha}$
ERROR C	180	σ^2_e

Σ represents fixed effect.
All variance components (σ^2) are described in model (2-1).
Coefficients: $c_1 = 3$, $c_2 = 6$, $c_3 = 16$, $c_4 = 24$, $c_5 = 48$, $c_6 = 144$ (assuming a balanced design).

where Y_{tijkm} is the mean of up to 5 trees (if living) in the m^th family of the k^th taxon in the j^th block of the i^th treatment at the t^th site,

μ is the population mean,

s_t is the random variable for site ~*NID* (0, σ^2_s),

α_i is the fixed effect for treatment (High *vs.* Low),

$s\alpha_{ti}$ is the random interaction site by treatment ~*NID* (0, $\sigma^2_{s\alpha}$),

$b_{j(ti)}$ is the random variable for block within site and treatment ~ *NID* (0, σ^2_b),

τ_k is the fixed effect for taxon (PEE, PEU or PTA),

$s\tau_{tk}$ is the random interaction site by taxon ~*NID* $(0, \sigma^2_{s\tau})$,

$\alpha\tau_{ik}$ is the fixed effect for the interaction treatment by taxon,

$s\alpha\tau_{tik}$ is the random three way interaction site by treatment by taxon ~ *NID* $(0, \sigma^2_{s\alpha\tau})$,

$b\tau_{ijkt}$ is the random interaction block(site and treatment) by taxon ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_{f})$,

$sf_{tm(k)}$ is the random interaction for site by family ~*NID* $(0, \sigma^2_{fs})$,

$\alpha f_{im(k)}$ is the random interaction treatment by family ~*NID* $(0, \sigma^2_{f\alpha})$,

$s\alpha f_{tim(k)}$ is the random three way interaction site by treatment by family within taxon ~ *NID* $(0, \sigma^2_{s\alpha f})$,

e_{tijkm} is the error term ~*NID* $(0, \sigma^2_{e})$;

where t=1,...11 sites; i = 1,2 management treatments; j= 1,2,3 blocks; k= 1,2,3 taxa; and m=1,...16 families per taxon.

Since some treatment by taxon interactions were significant in the pooled analysis (Model 2-2), a third and final set of analyses consisted of ANOVAs performed for each treatment (High and Low), but pooled across sites to test for main and interaction effects in the high and low treatments as separate experiments. The model based on plot means for this pooled analysis was derived from the model (2-2), where the number of treatments (α_i) equals one. The model used was obtained by dropping all terms from (2-2) relating to treatment (i.e., dropping all terms with subscript *i*).

For all single site and pooled analyses, PROC GLM was used to test the significance of random effects (SAS Institute Inc. 1988). Significance levels and estimated means (using LSMEANS option) for fixed effects (treatment, taxon, treatment by taxon) were obtained from PROC MIXED with the Satterthwaite option (Littell *et al.* 1996). A default probability value of 0.05 was established to show significance unless otherwise specified. To compare taxa differences, single degree-of-freedom contrasts were also computed for both single site and pooled analyses. Specific null hypotheses for contrasts were: 1) There are no differences between improved slash and improved loblolly (PEE *vs.* PTA); and 2) There are no differences between improved and unimproved slash (PEE *vs.* PEU).

Effect of rust infection on height growth

Since significant differences in height growth were found among taxa, an analysis was performed to determine if rust infection was influencing growth and hence causing the height growth differences among the taxon and treatment combinations. The goal was to examine whether height growth differences between PTA and PEE or between PEE and PEU were due in part to rust incidence differences.

An analysis of individual tree data for height was performed by expanding model (2-2) to include an ad-hoc treatment-variable for rust as dummy variable. This dummy (binary) variable was created by assigning "0" to any tree free of rust and assigning "1" to any tree with at least one rust gall. Both raw data and standardized data (by the phenotypic variance) were used for analysis, but since the results were similar, only the analysis with raw data is presented. The analysis proceeded using PROC MIXED to solve the mixed model specifications with the covariance parameters (SAS Institute Inc.1996) obtained from ASREML (Gilmour *et al.* 1997). To perform the analysis of this large model, some of the three and four way interactions were deleted, and the final model was:

$$Y_{tijkmno} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + b\tau_{ijkt} + f_{m(k)} + sf_{tm(k)} + \alpha f_{im(k)} + r_o + sr_{to} + \alpha r_{io} + \tau r_{ko} + s\alpha f_{tim(k)} + s\alpha r_{tio} + \alpha\tau r_{iko} + fr_{om(k)} + br_{ijto} + s\alpha\tau r_{tiko} + e_{tijkmno} \qquad (2\text{-}3)$$

where many effects are as described in model (2), and the remaining effects are:

$Y_{tijkmno}$ is the nth observation of the height on a tree with a oth rust damage in the mth family of the kth taxon in the jth block of the ith treatment at the tth site,

r_o is the dummy effect for rust (0= healthy and 1= presence),

sr_{to} is the random interaction site by rust ~*NID* $(0, \sigma^2_{sr})$,

αr_{io} is the fixed effect for the interaction treatment by rust,

τr_{ko} is the fixed effect for the interaction taxon by rust,

$s\alpha r_{tio}$ is the three way random interaction site by treatment by rust ~*NID* $(0, \sigma^2_{s\alpha r})$,

$\alpha\tau r_{iko}$ is the three way random interaction treatment by taxon by rust ~*NID* $(0, \sigma^2_{sr})$,

$fr_{om(k)}$ is the random interaction family within taxon by rust ~*NID* $(0, \sigma^2_{fr})$,

br_{ijto} is the random interaction block (site by treatment) by rust ~*NID* $(0, \sigma^2_{br})$,

$s\alpha\tau r_{tiko}$ is the four way random interaction site by treatment by taxon by rust ~*NID* $(0, \sigma^2_{s\alpha\tau r})$,

$e_{tijkmno}$ is the random error ~*NID* $(0, \sigma^2_{e})$.

Results and Discussion

Treatment Differences

Third-year survival

No significant differences were detected in third-year survival for any main effect or any interaction. However, when averaged across 10 sites and the three taxa, the high treatment had lower survival than the low treatment (92 *vs.* 95%).

Third-year rust infection

The pooled analysis showed no significant differences between treatments (Table 2-4). Averaged across 11 sites, the high treatment had more infected trees than the low treatment (33.6 *vs.* 29.2%), and considering the 9 sites with more than 15% rust incidence, the averages were 39 *vs.* 34.5% in the high and in the low treatment, respectively.

The effect of management treatment on rust incidence was inconsistent across sites. In 8 of the 11 sites, trees in the high treatment had more rust than in the low treatment, and this difference was significant in four installations. The low treatment had more rust on three sites, and the differences were significant in two sites (Appendix C). This inconsistency led to non-significant main effect for treatment in its overall effect on rust and significant site by treatment interaction.

It has been noted that fertilizer may predispose pines to infection by promoting more growth and hence succulent tissue (Schmidt *et al.* 1981; Anderson *et al.* 1984). In general, these results weakly support the general notion that site preparation and intensive culture increase the incidence of fusiform rust (Miller 1977; Burns *et al.* 1980; Burton and Snow 1983; Burton *et al.* 1985; Hood *et al.* 1988; Shoulders *et al.* 1990; Schmidt *et al.* 1995).

Table 2-4. Analysis of third-year data pooled across sites and management levels for rust incidence and height.

Source	RUST			HEIGHT		
	DF	F value	Pr > F	DF	F value	Pr > F
SITE	8	3.16	0.0486	9	3.80	0.0273
TREATMENT (H *vs.* L)	1	1.47	N.S.	1	23.66	0.0009
SITE*TREATMENT	8	5.88	0.0001	9	14.27	0.0001
TAXON	2	25.26	0.0001	2	62.76	0.0001
PEE *vs.* PTA	1	14.69	0.0004	1	61.35	0.0001
PEE *vs.* PEU	1	11.00	0.0017	1	9.47	0.0041
SITE*TAXON	16	1.99	0.0756	18	1.80	N.S.
TREATMENT*TAXON	2	0.01	N.S.	2	10.90	0.0007
SITE*TREAT*TAXON	16	3.13	0.0001	18	1.49	N.S.
FAMILY(TAXON)	49	9.07	0.0001	49	4.66	0.0001
SITE*FAMILY(TAXON)	356	1.27	0.0115	401	1.23	0.0196
TREAT*FAMILY(TAXON)	49	0.96	N.S.	49	1.33	0.0737
SITE*TREAT*FAMILY	356	0.91	N.S.	401	1.14	0.0461
ERROR	1682			1797		

ANOVA for rust was for the nine sites with more than 15% of rust.

Height

Single site analyses showed that in all sites, the high treatment significantly increased height growth (Appendix D). In other words, 10 out of 10 organizations effectively increased third-year height growth by increasing cultural management intensity. The pooled analysis showed the high intensive management increased ($p<0.01$) height growth from 2.60 m (in the Low) to 3.41 m (in the High), a 31% increase averaged over all 10 sites (ranging from 10 to 72% at individual sites). The significant site by treatment interaction ($p=0.0001$ in

Table 2-4) was due to scale effects, since there were no sites where the high treatment had shorter trees on the average than the low treatment.

Taxon Comparisons

Third-year survival

Overall, loblolly pine (PTA) had higher survival than both improved and unimproved slash pine (PEE and PEU). No significant site by taxon or treatment by taxon interaction was detected. Across 10 sites and both treatments, mean survival was 96.4% for PTA, 93.4% for PEE, and 90.7% for PEU. Single degree of freedom contrast analysis showed that PTA had higher survival than PEE in both treatments (95.5 *vs.* 91.9% in the high treatment, $p<0.02$, and 97.4 *vs.* 94.8% in the low treatment, $p<0.06$). PEE had better survival than PEU in both treatments ($p<0.03$).

Third-year rust infection

In both treatments, PEE and PEU were consistently more infected by fusiform rust at every site than PTA (Figure 2-1). No rank changes were detected due to site by taxon or treatment by taxon interactions in any pooled or single site analyses. Pooled analysis revealed highly significant taxon differences (Tables 2-4 and 2-5). Overall, PEE had nearly twice the rust incidence of PTA (as indicated by the ratio of slopes in Figure 2-1). The two slopes 0.71 for PEE regressed on PEU and 0.39 for PTA regressed on PEU were significantly different in a regression analysis. Further, improved slash (PEE) had consistently less rust than unimproved slash. PEE *vs.* PEU contrasts were significant in all pooled analyses ($p<0.003$).

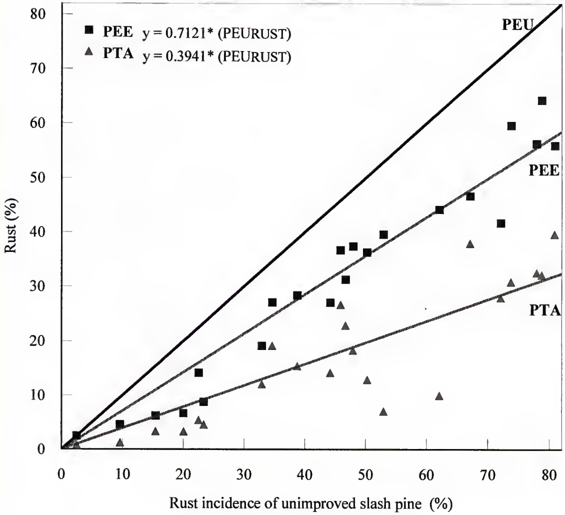


Figure 2-1. Rust incidence at 11 sites x 2 treatments (22 data points) at three years of age for slash pine (PEE) and loblolly pine (PTA) plotted against the rust incidence of unimproved slash pine (PEURUST). For the model y=PEURUST + PEURUST*TAXON, $R^2 = 0.91$. Treatment effect and interaction with other independent variables were non significant.

Table 2-5. Significance levels for rust incidence and height of third-year data pooled across sites, but analyzed separately by treatment.

Treatment / Source	RUST			HEIGHT		
	DF	F value	Pr > F	DF	F value	Pr > F
HIGH TREATMENT						
SITE	8	11.13	0.0001	9	35.03	0.0001
TAXON	2	28.01	0.0001	2	59.21	0.0001
PEE *vs.* PTA	1	16.95	0.0002	1	54.09	0.0001
PEE *vs.* PEU	1	11.66	0.0013	1	10.98	0.0024
SITE*TAXON	16	1.72	0.0851	18	1.79	0.0584
FAMILY(TAXON)	49	5.17	0.0001	49	4.41	0.0001
SITE*FAMILY(TAXON)	356	1.06	N.S.	401	1.30	0.0008
ERROR	810			898		
LOW TREATMENT						
SITE	8	12.96	0.0001	9	20.16	0.0001
TAXON	2	22.75	0.0001	2	32.86	0.0001
PEE *vs.* PTA	1	12.81	0.0009	1	35.56	0.0001
PEE *vs.* PEU	1	10.26	0.0027	1	3.25	0.0825
SITE*TAXON	16	2.77	0.0047	18	2.75	0.0030
FAMILY(TAXON)	49	5.51	0.0001	49	3.21	0.0001
SITE*FAMILY(TAXON)	356	1.10	N.S.	401	1.23	0.0069
ERROR	810			899		

ANOVA for rust was for the nine sites with more than 15% of rust.

Some authors have reported that loblolly pine is more rust susceptible than slash when growing in north Florida (Powers 1975; Kellison *et al.* 1979; Schmidt *et al.* 1986). This was not the case here. In those papers, unimproved and unknown levels of improved loblolly pine trees were studied.

No significant effect of treatment was detected on the ratios of PEE/PEU and PTA/PEU for rust infection, suggesting that the infection ratios of tolerant over susceptible materials remained constant when treatment intensity changed. Hodge *et al.* (1993a) showed that the same relative improvement for rust resistance was maintained at all levels of rust hazard for slash pine genotypes of different resistance levels. The non-significant effect of treatment on the ratios of PEE/PEU and PTA/PEU suggests a proportional rust resistance in both treatments. The PEE/PEU ratio was 0.71 and the PTA/PEU ratio was 0.39 (Figure 2-1). For example, PEE would have 42% rust infected trees on a 60% hazard site (0.71 x 60%=42%), whether the site received low or high intensity management. This implies that silvicultural treatments may increase rust incidence without influencing the relative resistance of improved material of these pines.

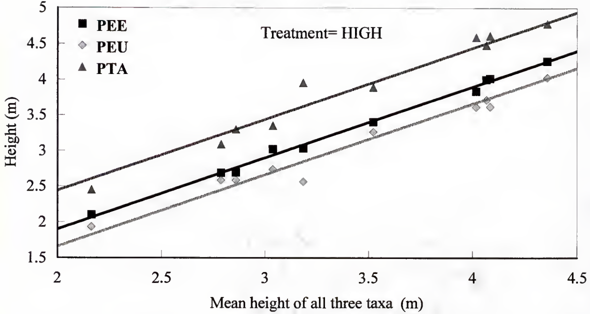
The R50 values (i.e., when rust incidence of PEU = 51.8% see Appendix A) calculated from the equations in Figure 2-1 were 36.8% for PEE and 20.2% for PTA. The R50 for a particular genotype estimates its expected percentage of rust infection on a site where unimproved material incurs 50% infection (Hodge *et al.* 1990a). The observed R50 value for PEE of 36.8% agrees with the *a-priori* prediction of 36% (see Material and Methods), and suggests that the breeding values predicted from best linear unbiased prediction indeed provide unbiased estimates of genetic gain (White and Hodge 1988).

Furthermore, the difference between PEU and PEE of 29% (average of 50% to 35.5%, Figure 2-1) in rust incidence clearly demonstrates that the advances in breeding to reduce the impact caused by this pest were effective. In fact, the incidence of rust predicted for the offspring of PEE was 37.1% when the PEU was 50% infected. In southeastern USA tree improvement programs, first-generation rust resistant selections have shown about a 30-35% reduction in rust incidence compared to unimproved seedlings (Schmidt *et al.* 1981; Powers and Kraus 1986; Hodge *et al.* 1990b). These results, reaffirm the success of genetic improvement on fusiform rust incidence by the CFGRP breeding strategy (Dhakal *et al.* 1996).

Height

Improved loblolly pine was consistently taller at three years of age than both improved and unimproved slash pine in both treatments and in all sites (Table 2-4, 2-5, Appendix D). The taxon by treatment interaction was significant and due to scale effects. This is evidenced graphically by larger differences among lines (taxa) in high *versus* low treatment (Figure 2-2). This result suggests that taxon differences were expressed more clearly in the high treatment (Figure 2-3). For example, the difference between PTA and PEE was 17% in the high treatment and 14% in the low treatment. Figure 2-2 demonstrates a parallel response to increases in site quality by the three different taxa (i.e., the slopes for all taxa are the same); however, the taxon differences for height growth increased in the high treatment. In average across sites, all PTA families were superior to the best PEE family for both treatments.

The fact that loblolly pine outperformed slash pine in the operational management regime does not support the generally accepted species-site relationship noted in other studies (Cole 1975; Colbert *et al.* 1990). It has been mentioned that in poorly drained soils, slash pine is more productive than loblolly (Cole 1975). In this research, most sites with poor



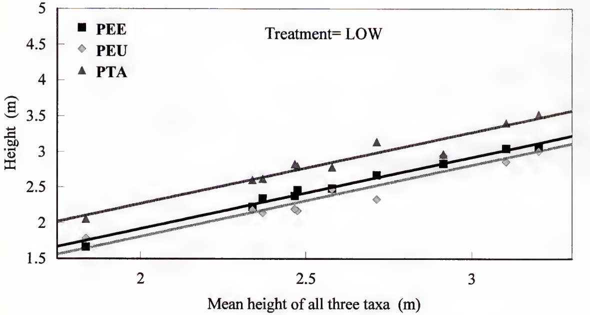


Figure 2-2. Total height by taxon across 10 sites at three years of age in the two treatments tested. Each point represents the mean of one taxon at one site. The x-axis is the mean height of the three taxa in each site-treatment combination. The lines were drawn from a regression considering the total height as dependent variable and the average of these taxa (mean height) as independent variable. Treatment and taxon effects were included in the model as class variables, which were significant, but slopes were not significantly different than 1. $R^2 = 0.98$. Thus, the six lines (2 treatments * 3 taxa) were drawn by the equation y= a + Mean height, where a= 0.44, -0.10, -0.34 for PTA, PEE and PEU in the high treatment, and a=0.27, -0.08, -0.29 for PTA, PEE and PEU in the low treatment.

drainage were bedded. Bedding wet sites before planting pines in the poorly drained flatwoods improves drainage, which improves early pine growth (Outcalt 1984; Gent *et al.* 1986; Shiver *et al.* 1990). Outcalt (1984) concluded that usually loblolly pine is more responsive to bedding than slash pine at this early stage of stand development, and this may explain the superior performance of loblolly pine in this study.

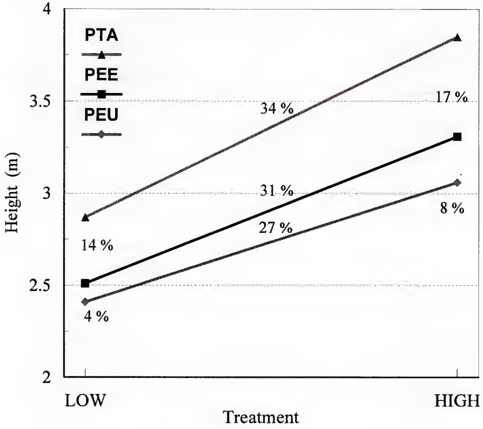


Figure 2-3. Third-year height by taxon in the two intensity of cultures. Taxon differences for height in percentage for PTA *vs*. PEE and PEE *vs*. PEU are shown on the left and right side for the Low and High treatment, respectively. The response of each taxon (in %) to the increasing intensity of culture is shown in central part.

It is unwarranted to draw general conclusions from such early growth (three years); however, overall, these results agree with the recommendations of Borders and Harrison (1989), who concluded based on eight-year data from "operational" conditions (without fertilization and bedding), that loblolly pine would be better suited on CRIFF soil groups A, D, F, and G (see Jokela *et al.* 1991 for soil types). On CRIFF B and C group soils they suggested that the two species were similar. There were no sites with CRIFF soil type B included in this research, but two sites had type C soils and PTA was taller than PEE ($p<0.02$, Table 2-1 and Appendix D).

Improved slash pine (PEE) was taller than unimproved slash pine (PEU) in 10 of 10 sites in the high treatment and in eight of 10 sites in the low treatment (Figure 2-2). In single site analyses, PEE was significantly taller than PEU in six and three of 10 sites for the high and low treatments, respectively (Appendix D, $p<0.05$). PEE had a larger response to cultural treatments than PEU. Thus, the average difference in height between PEE and PEU was larger for the high treatment pooled analysis (PEE 8% taller than PEU , $p=0.0024$, Table 2-5) than in the low treatment pooled analysis (PEE 4% taller, $p=0.08$). In average across sites, 11 and 9 out of 18 PEE families were superior to the best PEU family in the high and low treatments, respectively.

Rust influence on species comparison and realized gains in third-year height

Overall, trees without rust (0) were taller than trees with rust galls (1) ($p<0.03$, Table 2-6). This response was similar in both treatments, although more apparent in the low treatment (Figure 2-4). The taxa did not respond equally to rust. No significant differences

Table 2-6. Significance levels for rust effects and contrasts for third-year height growth. Analysis was done by adding a post-hoc treatment (called Rust) to each plot by assigning a 0 or 1 to trees without and with rust and then analyzing data for height. Pooled analysis was done combining data across both treatments.

Effect / Contrast	Pr > F		
	BOTH Treatments	HIGH Treatment	LOW Treatment
TAXON			
PEE *vs.* PTA	0.0001 -	0.0001 -	0.0111 -
PEE *vs.* PEU	0.0162 +	0.0044 +	N.S.
RUST (0 *vs.* 1)	0.0267 +	0.0592 +	0.0274 +
TAXON*RUST			
PEE*rust (0, 1)	0.0158 +	0.0286 +	0.0298 +
PEU*rust (0, 1)	0.0071 +	0.0189 +	0.0125 +
PTA*rust (0, 1)	N.S.	N.S.	N.S.
PEE-0 *vs.* PTA-0	0.0001 -	0.0001 -	0.0001 -
PEE-1 *vs.* PTA-1	0.0001 -	0.0001 -	0.0001 -
PEE-0 *vs.* PEU-0	0.0378 +	0.0098 +	N.S.
PEE-1 *vs.* PEU-1	0.0167 +	0.0072 +	N.S.

* 0 = no rust, 1= trees with rust. + = the 1st element is taller than the 2nd; - = the 2nd is taller than the 1st element.

in height were found between trees of PTA with and without rust as indicated by the lack of significance of PTA by rust interaction (Table 2-6). Both PEE and PEU were shorter when rust infected ($p<0.03$) and this was consistent in both treatments as indicated by the significant PEE and PEU by rust contrasts. However, since only total rust infection was measured, it is possible that in the "1" rust category, there were some trees with branch galls whose height was not affected. In larger trees (12 years) loblolly and slash pine trees were

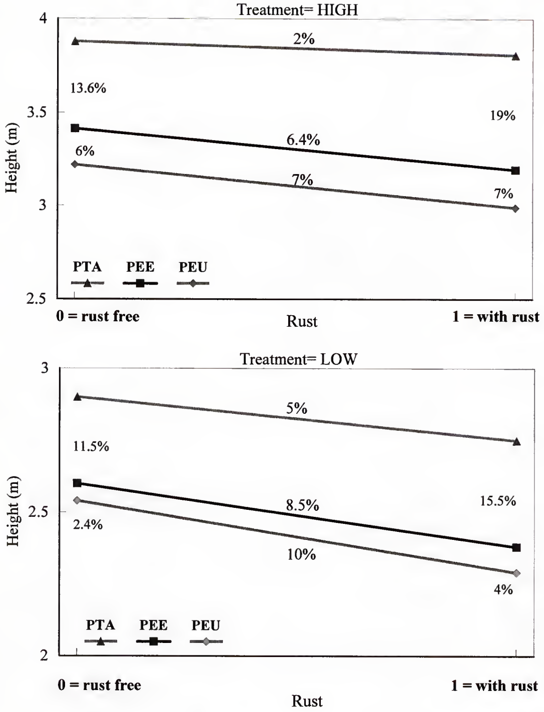


Figure 2-4. Third-year height by taxon and rust category in the two treatments tested. Each point represents the mean of one taxon-rust-treatment combination. The x-axis represents the two classes of rust presence, where 0 indicates trees free of rust and 1 trees with a least one rust gall. Reductions in height (in %) due to rust are indicated in the central portion of the lines. PTA-PEE and PEE-PEU differences are indicated on the left side (no rust) and on the right side (with rust).

both affected in growth by stem galls, though loblolly pine less than slash pine (Brawner 1998).

The significant contrast PEE-0 *vs.* PTA-0 in both treatments implies that the superiority of loblolly pine early height growth could not be totally attributed to less rust infection. In other words, if both species were planted in sites free of rust, PTA would be taller than PEE at 3 years of age. Further, the significant contrast PEE-1 *vs.* PTA-1 indicates that rusted loblolly pine were significantly taller than slash pine with rust. However, the differences between loblolly and slash pine height were affected. Without rust PTA was 12% taller than PEE, while with rust the difference was 17.6%. Although the three-way interaction of treatment by taxon by rust was not significant, the difference between PTA and PEE in height growth (Figure 2-3) were greater in the high treatment (0=13.6% and 1=19%) than in the low treatment (0=11.5% and 1=15.5%).

The realized gains of slash pine (PEE *vs.* PEU) for height growth were altered by the presence or absence of rust and the intensity of the silviculture (High *vs.* Low).Comparing only uninfected trees (PEE-0 *vs.* PEU-0) or infected trees (PEE-1 *vs.* PEU-1), gains for height were significant in the pooled (both treatments, $p<0.04$) and in the high treatment ($p<0.01$, Table 2-6).

In the previous analysis containing all trees, the difference between PEE and PEU for height was marginally significant in the low treatment ($p= 0.08$, Table 2-5). In this analysis with rust as a post-hoc treatment, no significant differences in height were found in the low treatment for either infected (PEE-1 *vs.* PEU-1) or uninfected trees (PEE-0 and PEU-0). Although, in the low treatment improved trees were taller than unimproved trees

2.4% and 4% with and without rust, respectively (Figure 2-4). Meanwhile, in the high treatment differences in height were 6% with no-rust and 7% with rust. Thus, at this early age, the gain of slash pine in height growth was consistent for both rust-infected and rust-free trees, but the height differences were most clearly expressed in the high intensive management treatment.

Conclusions

1. The results at three years of age showed that loblolly pine was consistently taller with less rust incidence than slash pine in both high and low intensity cultures on all sites tested. The early superiority of loblolly pine was partially due to its lower rust incidence, i.e., rust-free trees of loblolly pine also grew taller than rust-free trees of slash pine.
2. The increase in cultural management intensity did not alter the ratios of infection. That is, when the infection percentages of any two taxa were expressed as a ratio, it was essentially constant across all sites and in both silvicultural treatments.
3. Significant gain in rust resistance from selection and breeding was detected at this age on slash pine. When rust infection of unimproved slash pine is equal to 50%, improved slash pine was 36.8% infected. Through best linear prediction, the rust breeding value for improved slash was *a-priori* estimated at 36%, which proved an accurate prediction.
4. For all three taxa, the more intensive silvicultural treatment increased third-year height growth on all sites. Differences among taxa were also increased, because improved loblolly pine was more responsive than improved slash pine, which in turn was more responsive than unimproved slash pine.

CHAPTER 3
EFFECT OF SITE AND INTENSIVE CULTURE ON FAMILY DIFFERENCES IN EARLY GROWTH AND RUST INCIDENCE OF LOBLOLLY AND SLASH PINE

Introduction

Loblolly pine (*P. taeda* L.) and slash pine (*Pinus elliottii* Engelman var. *elliottii*) are the two most important commercial timber species in the southeastern United States (Borders and Harrison 1989). Several studies have examined the response of loblolly and slash pine to cultural practices at levels considered "operational" by forest industries, but few have included intensive silviculture (e.g., Haines and Gooding 1983; Blakeslee *et al.* 1987; Colbert *et al.* 1990). Such comparisons are important, because of the increasing interest in intensive culture to produce larger volumes of wood per unit area (Hagler 1996).

Moreover, there are few instances where genetic improvement has been incorporated into studies with both fertilization and weed control to compare the best available genotypes of both species (Borders and Harrison 1989; Swindel *et al.* 1988; Neary *et al.* 1990). Fertilization and competition affect growth and can increase susceptibility to physical damage and pest incidences on trees in both loblolly and slash pine, e.g., fusiform rust, caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* (Blakeslee *et al.* 1987; Miller and Schmidt 1987; Swindel *et al.* 1988; Shoulders *et al.* 1990). Genotypes may respond differentially to these challenges in disparate silvicultural treatments.

Genetic parameters such as family variances, heritabilities and the interaction of family with environment may also be affected by cultural practices. For example, heritabilities are greatly influenced by environmental homogeneity of the test environment, and homogeneity may be impacted by management activities. Further, since heritabilities are population-specific, studies with high and low intensity of silvicultural treatments may provide a good opportunity to explore how genotypes within species respond to culture by examining genetic expression and genotype by environment interaction for some traits.

There are many estimates of heritabilities for these species, for height growth (Hodge and White 1992; Balocchi *et al.* 1993; Bridgwater and McKeand 1997), and resistance to fusiform rust (Rockwood and Goddard 1973; Sohn and Goddard 1979; Hodge *et al.* 1990b; Dieters *et al.*1996). There is less information on the impact of silvicultural management on heritabilities in both loblolly and slash pine (Li and McKeand 1989; Surles *et al.* 1995; McKeand *et al.* 1997).

The specific objectives of this chapter are to: 1) Estimate heritability (h^2) for third-year height growth and resistance to fusiform rust and examine whether heritability is affected by management intensity under two levels of cultural practices across 11 sites in the lower Coastal Plain of USA; and 2) Examine patterns of environment by family interaction across these sites and management intensities to determine whether intensive culture affects family ranking in improved loblolly (PTA), improved slash (PEE) and unimproved slash pine (PEU).

Materials and Methods

Taxa description, seed collection, seedling production and field implementation are fully described in Chapter 2. Data from three taxa, improved slash pine, unimproved slash pine, and improved loblolly pine planted in 11 field test locations in the lower Coastal Plain of the southeastern USA are analyzed here in chapter 3. At each site, two cultural management intensities were established, intensive, labeled as High, and less intensive, Low.

The improved slash taxon (PEE) consisted of open-pollinated seed from 18 slash pine trees which were outstanding for volume growth or disease resistance. Since these families were open-pollinated, the average breeding values for the seedlots were calculated considering the breeding values of the clones (female parents) and all trees in the seed orchard (assuming 30% pollen contamination). The PEE seedlot was estimated to have means of 18.3% for volume gain and 37.1% for rust (R50), as predicted by the CFGRP (Appendix A). The 18.3% volume gain is expressed for 15-year volume above unimproved material. Lower R50 values indicate more resistance to fusiform rust (White and Hodge 1988; White *et al.* 1988). For example, a breeding value of 37% means that on a given site where unimproved material exhibit 50% rust infection, the PEE families are predicted to average 37% infection.

The unimproved slash pine families (PEU) consisted of open-pollinated seed from 17 parents intended to represent slash pine as it existed in 1955, before domestication. For comparison, the PEU seedlot was estimated to have a 4.9 % volume gain and an R50 of 51.3%. When comparing 15-year volume gain of the two taxa, the PEE is expected to have

1.183/1.049=12.7% more volume than PEU. Likewise, the rust infection of PEE at any age is predicted to be 37.1/51.3= 0.72 times the infection of PEU. For example, if PEU has 50% of the trees infected, PEE infection is predicted to be (0.72) x (0.50) = 36% (Hodge *et al.* 1993a).

The improved loblolly taxon (PTA) consisted of open-pollinated seed from 17 superior parents mostly from the Atlantic Coastal Plain. Details are not available on breeding values of these parents. Sixteen families in each taxon were planted per location. Overall, 18 PEE, 17 PEU and 17 PTA families were represented in these 11 tests, while 11 PEE, 15 PEU and 14 PTA families were common to all sites.

Variables Measured

The following variables were measured:

1. Height was assessed at three years old in the winter of 1997-98, and was measured as height to the highest terminal bud.
2. Rust incidence was assessed in the winter of 1997-98 (year 3) and scored as 0 (absence of rust) and 1 (presence of rust, either stem or branch galls).

Statistical Analysis

Data editing and standardization

Rust incidence data from eleven sites were obtained. However, two sites with less than 15% of the trees infected were excluded because the very low rust incidence levels have small variances (White and Hodge 1987). Data from ten sites were used for height analyses. One site was eliminated from the height analyses due to extensive deer damage, resulting in large experimental error for third-year height. For height analyses, an average of 2.5% of the data points in each block were outliers, distinctly outside the range of measurements. These were assumed to be inbred trees or recording errors, and were deleted prior to analysis (Mosteller and Tukey 1977).

To remove the effects of scale, height was standardized by dividing each observation in a site-treatment-block combination by the corresponding square root of the phenotypic variance for that block (Visscher *et al.* 1991, Hodge *et al.* 1996). These values were estimated through PROC MEANS (SAS Institute Inc. 1988).

General analysis of variance

All analyses of variance (ANOVA) were performed based on individual tree data. The model was:

$$Y_{tijkmn} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + b\tau_{tijk} + f_{m(k)} + sf_{tm(k)} + \alpha f_{im(k)} + s\alpha f_{tim(k)} + bf_{tijm(k)} + e_{tijkmn} \quad (3\text{-}1)$$

where Y_{tijkmn} is the n^th^ tree observation in the family m^th^ of the k^th^ taxon in the j^th^ block of the i^th^ treatment at the t^th^ site,

μ is the population mean,

s_t is the random variable for site ~*NID* $(0, \sigma^2_s)$,

α_i is the fixed effect for treatment (High *vs.* Low),

$s\alpha_{ti}$ is the random interaction of site by treatment ~*NID* $(0, \sigma^2_{s\alpha})$,

$b_{j(ti)}$ is the random variable for block within site and treatment ~ *NID* $(0, \sigma^2_b)$,

τ_k is the fixed effect for taxon (PEE, PEU or PTA),

$s\tau_{tk}$ is the random interaction of site by taxon ~*NID* $(0, \sigma^2_{s\tau})$,

$\alpha\tau_{ik}$ is the fixed effect for the interaction treatment by taxon,

$s\alpha\tau_{tik}$ is the random three-way interaction of site by treatment by taxon ~ *NID* $(0, \sigma^2_{s\alpha\tau})$,

$b\tau_{tijk}$ is the random interaction block within site and treatment by taxon ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$,

$sf_{tm(k)}$ is the random interaction of site by family within taxon ~*NID* $(0, \sigma^2_{sf})$,

$\alpha f_{im(k)}$ is the random interaction of treatment by family within taxon ~*NID* $(0, \sigma^2_{\alpha f})$,

$s\alpha f_{tim(k)}$ is the random three way interaction of site by treatment by family within taxon ~ *NID* $(0, \sigma^2_{s\alpha f})$,

$bf_{tijm(k)}$ is the random interaction of block within site and treatment by family within taxon ~*NID* $(0, \sigma^2_{bf})$,

e_{tijkmn} is the error term ~*NID* $(0, \sigma^2_e)$;

where t = 1,...9 or 10 sites; i = 1,2 management treatments; j = 1,2,3 blocks; k = 1,2,3 taxa; m = 1,...16 families per taxon; and n = 1, ...5 trees per plot.

PROC GLM (SAS Institute Inc. 1988) was used to test the significance of site by family, treatment by family, and site by treatment by family interaction. After the general ANOVA, three analyses of variance were performed per trait, one for each taxon, to estimate the significance of family, site by family, treatment by family, and site by treatment by family interaction. The model was obtained by dropping the taxon effect from model (3-1) (i.e., dropping all terms with subscript *k*). Thus, the ANOVA for each taxon was performed with the model:

$$Y_{tijmn} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + f_m + sf_{tm} + \alpha f_{im} + s\alpha f_{tim} + bf_{tijm} + e_{tijmn} \qquad (3\text{-}2)$$

where all effects are as described in model (3-1).

Heritabilities

To estimate single-site heritabilities (h^2_B) for both rust resistance and third-year height growth for all combinations of sites, treatments, and taxa, single-site analyses were accomplished using the individual tree data. With so few families in each taxon, the goal in h^2 estimation was not to add to the wealth of existing estimates of heritabilities already in the literature for these species (Rockwood and Goddard 1973; Sohn and Goddard 1979; Hodge *et al.* 1990b; Hodge and White 1992; Balocchi *et al.* 1993; Dieters *et al.*1996; Bridgwater and McKeand 1997), but to assess how silvicultural management actions affected h^2_B.

Variance components were estimated by PROC MIXED with the restricted maximum likelihood method, REML (Littell *et al.* 1996). The model using individual data for each site-treatment-taxon combination was the following:

$$Y_{jmn} = \mu + b_j + f_m + bf_{jm} + e_{jmn} \qquad (3\text{-}3)$$

where Y_{jmn} is the nth tree observation of the mth family in the jth block,

μ is the population mean,

b_j is the fixed effect for blocks,

f_m is the random variable for family $\sim NID\ (0, \sigma^2_f)$,

bf_{jm} is the random interaction of block by family $\sim NID\ (0, \sigma^2_p)$,

e_{jmn} is the error term $\sim (0, \sigma^2_w)$;

where j = 1,2,3 blocks; m = 1,...16 families; and n = 1,...5 trees.

The open-pollinated families in each taxon were assumed to be half-sib families; hence, the variance component for families (σ^2_f) can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A) (Falconer and Mackay 1996). Actually, σ^2_f is upwardly biased when obtained from single site analyses due to the confounding effects of genotype by environment interaction ($\sigma^2_f = \frac{1}{4}\ \sigma^2_A + \frac{1}{4}\ \sigma^2_{AE}$) (Comstock and Moll 1963). A total of 66 estimates of h^2_B for rust (11 sites x 2 treatments x 3 taxa) and 60 estimates for h^2_B third year height (10 sites) were obtained as follows:

$$h^2_B = 4 * \sigma^2_f \ / \ \sigma^2_f + \sigma^2_p + \sigma^2_w \qquad (3\text{-}4)$$

For height, standardized values, as indicated previously were used. For rust untransformed data values of 0 and 1 were used to calculate heritabilities. Binary heritability or heritability with untransformed values ($h^2_{B\,0,1}$) is appropriate for traits of low heritability ($h^2 \leq 0.3$) and for traits of high heritabilities with mean incidence levels less than 75% (Lopes 1998). However, to obtain heritability estimates that are independent of the frequency of the trait, the binary heritability was converted to an underlying continuous scale, ($h^2_{B\ un}$) by Dempster and Lerner's (1950) method:

$$h^2_{B\,un} = [\, h^2_{B\,0,1} * p\,(1-p)\,] \,/\, c^2 \qquad (3\text{-}5)$$

where: $h^2_{B\,un}$ is the heritability on the underlying scale;

$h^2_{B\,0,1}$ is the individual heritability on the binary scale estimated from 0/1 data;

p is the percentage of rust infection in each site-treatment-taxon combination.

c is the ordinate of the normal density function at the threshold.

Linear regression analyses were used in an attempt to explain trends in height and rust heritabilities associated with treatments and site. For rust incidence, the 66 estimates of h^2_B were used as the dependent variable and various transformations and combinations of mean rust incidence, treatments, and taxa as regressors (Sohn and Goddard 1979). For height, the 60 estimates of h^2_B were used as the independent variable with combinations of mean height growth, treatments and taxa as regressors.

Further, for third year height, the ratio of h^2_B in high treatment to h^2_B in low treatment was calculated for each site and used as a dependent variable (h^2_B-High to h^2_B-Low, a value larger than 1 means that h^2_B is larger in high treatment at that site). The ratio of mean height in the high treatment to mean height in the low treatment was used as a measurement of effectiveness of the intensive silviculture treatment on each site in causing growth differences. Thus, effectiveness and various transformations of this ratio and in combination with taxa were used as independent variables. Heritabilities of zero were removed from the analysis.

Preliminary regressions indicated that the heritability for height was affected by management intensity. Thus, a linear regression was used to examine if the change in heritability was due to changes in genetic variance (additive variance) or environmental variance. First, to reduce dependence of these variances on scale, coefficients of variation (CV) were created for both additive and environmental error variances (CV-Add and CV-Error) as :

$$\text{CV-Add} = \frac{\sqrt{4 * \sigma^2_f}}{\text{height}} \quad \text{and} \quad \text{CV-Error} = \frac{\sqrt{\sigma^2_w - [3 * \sigma^2_f]}}{\text{height}},$$

where height = mean height of a given site-treatment-taxon combination.

Thus, for height 60 CV-Add and 60 CV-Error values were created (2 treatments x 10 sites x 3 taxa). For both CV-Add and CV-Error, a ratio of CV in the high treatment to CV in the low treatment was created to be the dependent variable (30 observations of CV-Add High to CV-Add Low, and 30 observations of CV-Error High to CV-Error Low). As before, effectiveness (mean of height in the high treatment to mean of height in the low treatment) was considered an independent variable for regressions with taxa as a class variable. Several models were tried to examine the importance of management treatments.

Genotype-by-environment interaction

First, due to the significant site by family and treatment by family interaction for third year height, several analyses were performed to investigate the variation among families and family x environment interaction. The goal was to determine if silvicultural treatments caused rank changes among families and if these rank changes across treatments were larger than rank changes of families across sites.

A change in relative performance across environments is called genotype x environment interaction (GxE). Estimates of type-B genetic correlations are widely used as a measure of GxE, in formulating breeding strategies and deploying genetically improved materials (White *et al.* 1993). Type-B genetic correlation was used to examine the stability of family performance across environments (Burdon 1977; Lu 1999). This correlation is defined as the genetic correlation for the same trait measured in different environments (Yamada 1962; Burdon 1977). The procedure for standardization for height trait (mentioned in Data editing and standardization) was used to homogenize phenotypic variances across tests and treatments (Dickerson 1962, Yamada 1962). Then, a genetic correlation near one indicates that interaction is negligible (i.e., family ranking are stable). On the other hand, a genetic correlation less than one implies changes in families ranking in different sites or treatments. Type B genetic correlations were estimated (r_B) (Yamada 1962) for each taxon as:

$$r_{B\text{-treat}} = \sigma^2_f / (\sigma^2_f + \sigma^2_{\alpha f}), \text{ and} \qquad (3\text{-}6)$$

$$r_{B\text{-site}} = \sigma^2_f / (\sigma^2_f + \sigma^2_{sf}) \qquad (3\text{-}7)$$

The goal was to investigate genetic expression within taxon and to determine how it was affected by site and management treatments. All analyses were done separately by taxon to see if trends were consistent for PEE, PEU and PTA. To estimate $r_{B\text{-treat},}$ the variance components for family and treatment by family (σ^2_f and $\sigma^2_{\alpha f}$) were obtained from a pooled analysis (model 3-2), but site, treatment, and block were considered fixed effects. To estimate $r_{B\text{-site}}$, one ANOVA was performed for each treatment-taxon combination (six ANOVAs in total) to investigate whether genetic correlations among sites were consistent across treatments and taxa. The variance components for family and site by family (σ^2_f and σ^2_{sf}) were obtained using the pooled analysis model (3-2), but treatment was dropped from the model (i.e., dropping all terms with subscript *i*). Thus the model was:

$$Y_{ljmn} = \mu + s_l + b_{j(l)} + f_m + sf_{lm} + bf_{ljm} + e_{ljmn} \qquad (3\text{-}8)$$

where all term were described in model 3-1, but site and block effects were considered as fixed effects and l = 1,...9 or10 sites; j = 1,2,3 blocks; m = 1,...17 or 18 families per taxon; n = 5 trees.

Where important GxE interaction existed (r_B <0.7, as suggested by Shelbourne 1972), several analyses were performed to identify the responsive families in each taxon or to find which sites were causing the GxE. Furthermore, some analyses were performed by including the effect of the seedling grower. Four seedling growers were used to supply the seedlings, and each grower produced the plants used in two or three test sites (Table 2-1). Each group of test locations that shared the same grower is denoted as a series. Series was added to model 3-8 and site was nested in series. To examine whether rust was causing the GxE on height, some analyses were done using only data from rust-free trees (rust = 0). Lastly, with series in the model and with data from rust-free trees, the GxE analyses were redone.

Finally, a relative gain estimation for third-year height growth was performed to compare gains from progeny testing in one culture and deployment in another culture. Relative genetic gains, which is the ratio of indirect gain to direct gain, for each taxon were calculated with the formula developed by Falconer and Mackay (1996). This ratio measures the relative gains from choosing families or parents based on their performance in Low and then planting those chosen families in High (or vice versa). For progeny testing in the Low intensity and deployment in High intensity culture, the final formula was derived from Relative Gain = Indirect gain / Direct gain as:

$RG_{L\,to\,H} = i_L\, r\, h_{fL}\, h_{fH}\, \sigma_H \ \ / \ \ i_H\, h^2_{fH}\, \sigma_H,$

Assuming that the intensity of selection is the same in both environments ($i_L = i_H$), the relative genetic gains for third-year height growth for comparing gains from progeny testing in low and deployment in high intensity were:

$$RG_{L\,to\,H} = r_{B\text{-}Treat} \ x \ (h_{fL} / h_{fH}) \qquad (3\text{-}9)$$

Similarly for progeny testing in high and deployment in low intensity:

$$RG_{H\,to\,L} = r_{B\text{-}Treat} \ x \ (h_{fH} / h_{fL}) \qquad (3\text{-}10)$$

where: $r_{B\text{-}Treat}$ is the type B genetic correlation for treatments averaged over all three taxa,

h_f is the square root of family heritability for height growth in High and Low culture (derived below).

Ratios of gains $RG_{L\,to\,H}$ and $RG_{H\,to\,L}$ were performed by pooling taxa (not conducted separately for each taxon). Since heritability estimates were based on few families, it was assumed that all taxa were similar and differences in estimates for PEE, PEU and PTA were errors from sampling a small number of families in each taxon. Thus, single-site heritabilities were taken as $h^2_{B\,H}$ =0.30 and $h^2_{B\,L}$=0.20. Then h^2_B has $4\sigma^2_F$ in numerator and $\sigma^2_F * r_{B\text{-}site} = \sigma^2_f$ and $\sigma^2_{fe} = \sigma^2_F - \sigma^2_f$ (White and Hodge 1992). Thus σ^2_f and σ^2_{fe} were substituted in :

$$h^2_f = \sigma^2_f \,/\, (\sigma^2_f + \sigma^2_{fe}/t + \sigma^2_e/tb) \qquad (3\text{-}11)$$

where: σ^2_f is the variance due to average family effects;

σ^2_{fe} is the variance due to family by environment interaction effects;

b is the number of blocks assuming single-tree plots.

To predict the ratios of relative gains, a simulation was performed substituting number of sites from 1 to 20 and assuming 15 blocks per site.

Results and Discussion

Family Effects and Interaction With Sites and Treatments

Rust incidence

Significant differences were found among families within taxa for rust incidence in all pooled analyses performed. The non-significant interaction of site by family in each treatment pooled analysis showed that families performed consistently across sites in both cultural treatments. This supports the results of many researchers, that genotype by environment interaction for fusiform rust infection is of little practical importance in either slash or loblolly pine (Kinloch and Stonecypher 1969; Goddard and Schmidt 1979; Wells *et al.* 1982; Hodge *et al.* 1990b, 1993a; Dieters *et al.* 1996). Also, no significant treatment by family interaction was detected, i.e., resistant families have less rust incidence than susceptible families whether growing in operational or intensively managed areas. Therefore, if considering only the rust incidence, deployment of families to intensive management sites may be based on their resistance evaluations like R50 (Hodge *et al.* 1993a), i.e., for most families there is no need for matching specific families to either sites or management regimes.

Height

Significant differences were found among families within taxa for height in all pooled analyses performed. On average across sites, all 18 PTA families were superior to the very best PEE family in both treatments (data not shown). Meanwhile, 11 and 9 out of 18 PEE families were superior to the best PEU family in the high and low treatments, respectively.

Treatment by family interaction was also significant in the pooled analysis. Site by family interactions were highly significant for height in both pooled analyses (pooling all three taxa and separately by taxon for models (1) and (2)). Genotype by site interaction for height has been noted to occur in slash pine progenies, where some progenies did not perform consistently in low, medium, and high productivity sites (Goddard and Rockwood 1982).

Heritabilities

Rust incidence

With so few families from selected parents, these heritabilities should be used with caution, although some conclusions may be drawn (Table 3-1). Regression analysis indicated that single-site rust heritabilities both for the untransformed values 0 and 1 ($h^2_{B\,0,1}$) and in the underlying scale ($h^2_{B\,und}$) were not affected by the change in management intensity; that is, no significant treatment effect was detected in regression analysis on either scale.

Table 3-1. Mean and range (in parentheses) single-site heritability values for rust by treatment and taxon. Heritability was obtained using 0-1 data ($h^2_{B\,0,1}$) and in the underlying scale ($h^2_{B\,und}$) by Dempster and Lerner's (1950) method.

		High Treatment		**Low Treatment**	
$h^2_{0,1}$	PEE	0.29	(0.0-0.61)	0.28	(0.0-0.57)
	PEU	0.17	(0.0-0.42)	0.13	(0.0-0.32)
	PTA	0.12	(0.0-0.35)	0.10	(0.0-0.47)
	Average	0.19		0.17	
h^2_{und}	PEE	0.38	(0.0-0.91)	0.40	(0.0-0.87)
	PEU	0.29	(0.0-0.66)	0.24	(0.0-0.59)
	PTA	0.20	(0.0-0.65)	0.21	(0.0-0.71)
	Average	0.29		0.28	

On the observed binary scale, the single-site heritabilities for rust ($h^2_{B\,0,1}$) were well predicted by a quadratic function of the mean rust incidence in the test including taxon as class variable (Figure 3-1). This behavior has been noted by other researchers when using heritability on the binary scale (Sohn and Goddard 1979; Hodge *et al.* 1990b, 1993a; Souza *et al.* 1991; Dieters *et al.* 1996). The predicted maximum biased heritability occurred at 60.5% of rust incidence which is close to that reported by Sohn and Goddard (1979) and Dieters *et al.* (1996). The maximum h^2 values were predicted to be 0.33 for PEE, 0.21 for PEU and 0.27 for PTA, but these differences among taxa may reflect the few families upon which the estimates are based and their different rust incidence.

The heritability on the underlying continuous scale ($h^2_{B\,und}$) is better for taxon comparisons, and the single site $h^2_{B\,und}$ are quite similar both among taxa and treatments (Table 3-1). In fact, when modeled as the dependent variable in the regression, $h^2_{B\,und}$ was not affected by the change in the management intensity nor environments. Regression analysis with 66 $h^2_{B\ und}$ estimates indicated a significant taxon effect, but a non-significant effect of management intensity. The taxon effect explained 12% of the variability among estimates of $h^2_{B\ und}$ (p=0.023). Although the site effect was significant (p=0.026), this effect explained only 0.2% of the variability among estimates of $h^2_{B\ und.}$

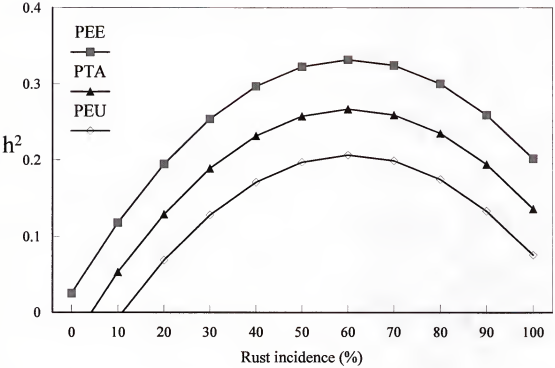


Figure 3-1. Predicted models for single-site heritability (h^2_B) of rust incidence for the three taxa tested. For the full model including taxon as a main effect the $R^2 = 0.40$. The final model is $h^2_{B\ 0,1} = a + 0.010133\ r - 0.00008371\ r^2$, where a is 0.0254, -0.1004 and -0.0398 for PEE, PEU and PTA, respectively, and r = rust incidence (in percent) at the site.

Height

Overall, the increase in management intensity increased single-site heritability as well as height growth (Table 3-2). An analysis of variance with the 60 estimates of h^2_b (2 treatments x 10 sites x 3 taxa) indicated that site and treatment were the only significant effects to explain h^2_b. This higher heritability for height growth in the high treatment implies that genetic gains may be improved through selection of genotypes under intensive management practices. For example through cultural practices, intensively managed tests have been successful in increasing juvenile mature correlations in *P. taeda* (Li *et al.* 1992).

Table 3-2. Mean and extreme single-site heritability estimates for height by treatment and taxon. Analyses were done with third-year data with standardized values obtained by dividing raw data by the square root of the phenotypic variance in each block.

TAXON	**High Treatment**		**Low Treatment**	
PEE	0.29	(0.08-0.57)	0.19	(0.00-0.44)
PEU	0.31	(0.00-0.47)	0.23	(0.00-0.54)
PTA	0.32	(0.04-0.46)	0.23	(0.09-0.49)
Average h^2_B	0.31	± 0.035	0.22	± 0.035

Both the additive variance and the error variance for height were lower in the high treatment. The reduction of additive variation (6% reduction in CV-ADD from 0.1891 in Low to 0.1783 in High) may be due to reduced genetic expression in the uniform environment. In any case, the environmental error was more strongly reduced with the increased intensity of management treatments (25% reduction in CV-Error from 0.3186 in Low to 0.2386 in High), and this resulted in increased h^2 values.

The effectiveness of the increased management intensity, measured as the ratio of mean height in High divided by mean height in Low at each site, was partially associated with the difference in h^2_B between High and Low (Figure 3-2). This was consistent for all three taxa since no significant taxon effect was detected in the regression analyses. The phenotypic correlation coefficient between the ratio of h^2_B in the High to h^2_B in the Low treatment and effectiveness was 0.61 (Table 3-3), and this ratio of heritabilities was positively associated with the ratio of the coefficient of variation for additive variance in High to the coefficient of variation for additive variance in Low (CV-Add High to CV-Add Low, r=0.66). The heritability ratio was negatively associated with the ratio of the coefficient of variation for environmental error in High to the coefficient of variation for environmental error in Low (CV-Error High to CV-Error Low, r= -0.73).

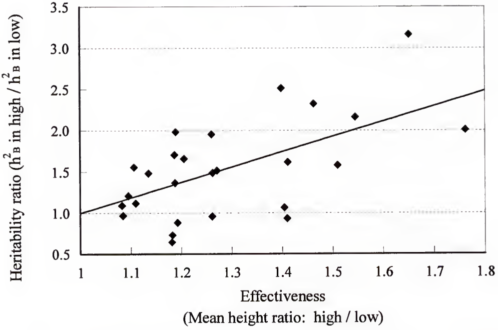


Figure 3-2. Single-site heritability ratio (h^2_B in High / h^2_B in Low) as a function of the effectiveness of cultural treatment. For the full model h^2_B-high / h^2_B-low = -0.86 + 1.86 (Effectiveness). $R^2 = 0.37$ and taxon was not significant as a regressor.

Table 3-3. Pearson correlation coefficients of heritability ratio for height, effectiveness, the ratio coefficient of variation for additive variance in High to coefficient of variation for additive variance in Low (CV-Add High to CV-Add Low), and the ratio coefficient of variation for environmental error in High to coefficient of variation for environmental error in Low (CV-Error High to CV-Error Low).

	Effectiveness (High / Low height ratio)	CV-Add High to CV-Add Low	CV- Error High to CV-Error Low
h^2_B High / **h^2_B** Low ratio	0.6070*	0.6562**	-0.7281**
CV-Add High to CV-Add Low	-0.1700$^{n.s.}$	--------	--------
CV- Error High to CV-Error Low	-0.9002**	-0.0736$^{n.s.}$	---------

** = P<0.001; * = P<0.01; N.S. = not significant.
n= 30 (3 taxa x 10 sites).

The intensive cultural treatment was effective in increasing heritability for height by decreasing the coefficient of variation for environmental error (CV-Error). The CV-Error High to CV-Error Low ratio was closely associated with a linear function of effectiveness (r = -0.90 in Table 3-3 and see Figure 3-3). No significant taxon effect was detected in the regression.

On the other hand, additive variance was not related to the effectiveness of the management intensity. That is, variation in the ratio of CV-Add High to CV-Add Low among sites and taxa was not explained by regressions including taxa or by a linear or quadratic function of effectiveness or any combination of them. Further, the correlation of effectiveness with the ratio of CV-Add High to CV-Add Low was -0.17 (Table 3-3).

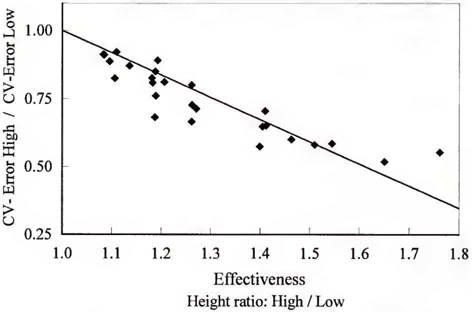


Figure 3-3. Predicted model for the coefficient of variation of environmental error expressed as a ratio of the High and Low management (CV-Error High / CV-Error Low) for height as a function of the effectiveness in the three taxa tested. For the full model: (CV-Error High / CV-Error Low) = 1.82 - 0.82 (Effectiveness), $R^2 = 0.81$. Taxon and taxon interaction with effectiveness were not significant. A value of >1 for effectiveness means that third-year height in the High treatment is larger than the height in the Low treatment.

Intensive silviculture, e.g., fertilization, drainage improvement, weed competition control, have been shown to reduce micro-environmental variation (Kiss and Yeh 1988; Bouvet and Vigneron 1995; Woods *et al.* 1995). Also, any kind of biotic or mechanical injury to the plants can also contribute to the large within-plot variance (Kiss and Yeh 1988). The insecticide application to reduce tip moth *(Rhyacionia* spp.) damage, greater control of weeds and fertilizer applications in the intensive treatment apparently reduced the environmental error and hence increased heritability for height growth.

Genotype-by-environment interaction

Rust incidence

In agreement with the non-significant treatment by family interaction in the ANOVA, type B genetic correlations for treatments ($r_{B\text{-treat}}$) indicate highly stable rankings for rust resistance across the two management intensities (Table 3-4). The selection of families for commercial plantations based on rust incidence may be done irrespective of silvicultural activities, i.e. increased management would not inordinately affect resistant families when compared to less resistant ones.

Table 3-4. Estimates of type B genetic correlation for rust incidence for both the site by family interaction and the treatment by family interaction. Values were obtained from equations 3-6 and 3-7 using nine sites with greater than 15% of rust incidence.

TAXON	$r_{B\text{-treat}}$	$r_{B\text{-site}}$	
		HIGH	LOW
PEE	1.0	1.0	0.96
PEU	0.95	0.86	0.93
PTA	0.96	0.85	0.83
Average	0.97	0.90	0.91

The estimates of type B genetic correlations for sites ($r_{B\text{-site}}$) indicate high stability of family rankings for rust resistance across sites (Table 3-4). Both treatments showed similar and very low levels of GxE, indicating that GxE is not important for rust. A similar result was found by Dieters *et al.* (1996), who stated that GxE interaction appeared to be of little importance for rust resistance in slash pine.

Height

Although caution is needed in drawing inferences with relatively few families, family rankings for height were less influenced by environmental differences among treatments than by differences among sites (Tables 3-5, and 3-6); this was consistent for all these taxa. Overall, values of type B genetic correlations for treatments ($r_{B\text{-treat}}$) indicate high stability of rankings for height across the two management intensities (Table 3-5). For both PEE and PTA one family (out of 18 and 17 for PEE and PTA, respectively) appeared more responsive to more intense silviculture (Appendix E and F). When this single family was dropped, the type B correlation estimates were 1.0 for PTA and 0.94 for PEE. Although evaluation at mature ages is necessary, the selection of families for commercial plantations at this age seems less influenced by silviculture activities.

Table 3-5. Estimates of type B genetic correlations for height for the treatment by family interaction. Values were obtained from equation 3-6.

TAXON	$r_{B\text{-treat}}$	
	RAW	Dropping the most responsive family
PEE	0.76	0.94
PEU	0.91	0.94
PTA	0.93	1.0
Average	0.87	0.95

Site by family interaction was high (low values of $r_{B\text{-site}}$), i.e., families were changing rank across sites (Table 3-6). GxE across sites may be very sensitive to the small number of trees per family planted in each site-treatment combination (5 trees x 3 blocks= 15 trees) and the arrangement in five-tree plots. However, the high treatment had less GxE. The larger genotype by environmental interaction in the low treatment indicates a lack of consistency in the relative performance of genotypes when growing in different environments (sites) under operational cultural conditions (Table 3-6). Conceivably, the intensive culture practices in high treatment ameliorated the site and may have removed some limiting factors. This may explain the smaller GxE in the High treatment.

Table 3-6. Estimates of type B genetic correlation for height for the site by family interaction. Values were obtained from equation 3-7 using standardized data in three different analyses: Including all trees (All); using only rust-free trees (Rust-free) and adding seedling grower to the model (Series). The value when dropping the most responsive single family in parentheses.

TAXON	$r_{B\text{-site}}$					
	HIGH			LOW		
	All	Rust-free	Series	All	Rust-free	Series
PEE	0.41 (0.63)	0.74 (0.81)	0.91 (1.0)	0.38 (0.61)	0.82 (1.0)	0.41 (0.75)
PEU	0.69 (0.75)	0.89 (0.99)	0.80 (0.87)	0.50 (0.67)	0.57 (0.61)	0.57 (0.69)
PTA	0.80 (0.94)	0.95 (1.0)	0.82 (0.97)	0.65 (0.76)	0.59 (0.67)	0.57 (0.69)
Average	0.63 (0.77)	0.80 (0.91)	0.84 (0.95)	0.51 (0.68)	0.66 (0.76)	0.52 (0.71)

Two other factors appeared to influence GxE for height: rust incidence and series (sites in same series were grown in the same nursery). In general, when trees free of rust were analyzed, GxE was lower ($r_{B\text{-site}}$) than when all trees were included and this was true for both management treatments (Table 3-6). Rust is known to affect height growth (Chapter

2) and differences among families in rust resistance could alter family rankings for height. When Series (seedling grower effect) was included in the model, GxE was significantly reduced for slash pine in the high treatment. This reduction in GxE was greater for the improved slash pine families. Apparently, seedling quality differences from the different growers carried over through three years in the filed altered family rankings among growers.

Relative gains in height growth

Additional genetic gain in early height growth is expected if family selection is performed in one single site managed with intensive culture followed by operational deployment in plantations managed with less intensive culture. This is due to higher h^2_B in the high treatment and the high $r_{B\text{-treat}}$. However, the relative benefit of testing families in intensive culture for deployment in operational culture ($RG_{H\,to\,L}$) decreases as the number of test locations increases (Figure 3-4). Therefore, with a large number of test locations, there is no benefit of testing families in intensive silviculture for subsequent planting under operational conditions. On the other hand, the relative benefit of testing families in less intensive for deployment in intensive culture increases as number of sites planted increases. The relative gains approach the same value from either direction as number of tests increases, and gains depend only on the treatment by genotype interaction ($r_{B\text{-treat}}$=0.87, Figure 3-4 with equation 3-11).

If the difference in height growth between intensive culture and operational plantations were large and GxE became large, it is conceivable that the increase in h^2 in intensive culture may not be enough to offset the reduced correlations (see equations 3-9 and 3-10). Thus, additional gains from testing in high intensity treatments could conceivably be nullified. In this study no evidence for the previous hypothesis was found. Even when the differences in early height growth between high and low treatments were on average 31% (from 10 to 72% at individual sites), the average $r_{B\text{-treat}}$ was 0.87. Furthermore, no significant factor was detected in regression analyses to corroborate an increase of GxE when treatment effectiveness increased to produce larger height differences between intensive and less intensive treatment. Further research is needed comparing intensive *versus* non-intensive culture and evaluation at mature ages is needed to corroborate these early results; however, the results suggest that all genetic tests could be managed intensively (to achieve higher heritabilities) even when planned culture of operational plantations is less intensive.

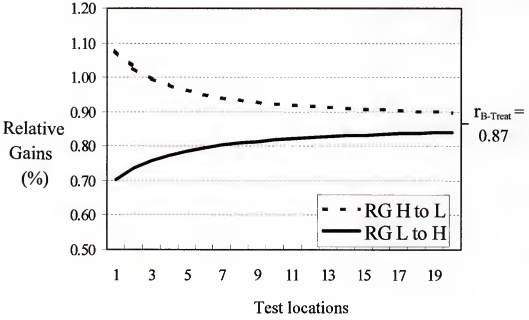


Figure 3-4. Predicted model for the relative genetic gains in early height growth from family selection if testing in high treatment to deploy in low treatment (RG H to L) and from testing in low treatment to deploy in high treatment (RG L to H). Values were obtained combining information across taxa with formula 3-11.

General Discussion and Conclusions

The type B genetic correlations ($r_{B\text{-site}}$=0.90 and $r_{B\text{-treat}}$=0.97) indicate highly consistent family rankings for rust incidence across sites and management intensities. This supports the results of many researchers, that genotype by environment interaction for fusiform rust infection is of little practical importance in either slash or loblolly pine (Kinloch and Stonecypher 1969; Goddard and Schmidt 1979; Wells *et al.* 1982; Hodge *et al.* 1990b, 1993a). Therefore, if considering only rust incidence, deployment of families in both intensive and operational management regimes may be done based on their resistance evaluations based on testing in either or both management regimes.

While these results for rust resistance suggest that there is no need to match specific families to either sites or management regimes, recent results based on a very small number of families indicated that slash pine families were not always stable in rust resistance across sites and planting years (Schmidt *et al.* 1999). Even though results with few families should be used with caution, decisions on single-family deployment in commercial plantations should consider potential instability for rust resistance.

With few families from selected parents (52 families in total for this experiment), the heritability estimates should be interpreted cautiously, although some conclusions may be drawn. Single-site heritabilities for rust in the binary scale ($h^2_{B\,0,1}$) and in the underlying scale ($h^2_{B\,und}$) were not affected by site nor by the increase in management intensity, even though rust incidence was somewhat increased by intensive management (Chapter2). Conversion to the underlying scale diminished parameter dependency on rust incidence and indicates a $h^2_{B\,und}$ of 0.29. This value is in the range of other estimates for single-site heritability for rust when transformed to the underlying scale by Dempster and Lerner's (1950) method ($h^2_{B\ und}$=0.26 in Rockwood and Goddard 1973; h^2_{Bund}=0.33 in Dierters *et al.* 1996). Taken together, these estimates indicate that rust resistance is one of the more heritable traits of commercial importance other than wood properties. From information on many studies, single-site heritabilities for growth traits range from 0.1 to 0.25, while for wood specific gravity h^2_B is above 0.3 (Cornelius 1994). So, resistance to fusiform rust is more heritable than most traits.

For third-year height growth, family rankings for height were less influenced by environmental differences in management intensity than by differences among sites; this was consistent for all three taxa ($r_{B\text{-treat}}$=0.87 while $r_{B\text{-site}}$=0.57, averaged over all three taxa). Although evaluation at mature ages is necessary, these early results imply that stable rankings for height may be expected when cultural intensity increases. However, a few families were more responsive, and these may be useful for deployment under intensive culture conditions.

Site by family interactions for height were significant and important (low values of $r_{B\text{-site}}$), meaning that families were changing rank across site. Some general observations may be drawn. First, loblolly pine families were more stable across sites than slash pine families (Table 3-6). Second, differences in rust incidences caused some instability in height rankings in the analysis across sites, because more resistant families had relatively better performance for height on highly infected sites. Third, seedling quality also affected the GxE. Height of improved slash pine seemed particularly sensitive to the different quality of seedlings from different growers. Fourth, the intensive culture had smaller site by family interaction (higher

$r_{B\text{-site}}$ value) than less intensive culture, meaning more stable family rankings across sites for intensive culture (Table 3-6). Conceivably, cultural practices in the intensive treatment ameliorated the site and may have removed some limiting factors. The decreased environmental differences across sites may have increased the apparent stability of genotypes.

The increase in management intensity increased average third-year height growth and its single-site heritability. Both additive variance and environmental error for height were lower in the intensive treatment. The reduction of 6% in additive variation may be due to reduced genetic expression in the uniform environment. In any case, the environmental error was more strongly reduced (by 25%) in the intensive management treatment and this resulted in higher heritability (h^2_B = 0.3 *vs.* 0.2, averaged over all three taxa in high and low, respectively). The greater control of weeds and insecticide applications to reduce tip moth *(Rhyacionia* spp.) damage in the intensive treatment may have contributed to the reduced environmental error and hence increased heritability for height growth for all three taxa.

The higher heritability for height growth in the intensive management treatment implies that genetic gains from progeny testing are higher in intensive culture (when selected families are deployed back to the environment in which they are tested). This means testing in intensive culture to deploy in intensive culture achieves more gain than testing in less intensive to deploy in less intensive. Moreover, this higher heritability in the intensive culture along with little GxE between treatments ($r_{B\text{-treat}}$=0.87, averaged over all three taxa) indicates that gains from indirect testing favor testing families in intensive management for subsequent deployment in operational management regimens. These conclusions for height growth need confirmation with later results since they are based on data at three years of age. However, it appears that progeny testing with intensive culture could have advantages for deployment in either culture, although as the number of sites increases, the advantage of testing in intensive culture decreases.

CHAPTER 4
TAXON AND FAMILY DIFFERENCES IN SURVIVAL, COLD HARDINESS, EARLY GROWTH, AND RUST INCIDENCE OF LOBLOLLY PINE, SLASH PINE, AND SOME SLASH PINE HYBRIDS

Introduction

Geneticists have long been aware that species hybridization has the potential to be a valuable approach in developing genetically-improved, domesticated tree varieties. Hybridization creates new gene combinations that can be captured and economically utilized (Fowler 1978). Many characters of hybrids are intermediate to both parents and others resemble those of one parent (Little and Righter 1965). Sometimes the crosses of two different genotypes produce hybrid vigor or heterosis, which is defined as an excess in vigor for the particular trait of the hybrid over the midpoint between its parents (Burton 1980). However, heterosis in forest tree species and provenance hybrids is the exception rather than the rule (Fowler 1978). Further, expression of hybrid vigor is dependent on environment, and sometimes due, apparently, to complementarity of desirable traits of the parents (Wright 1976; Nikles and Robinson 1988; Martin 1989).

Species hybridization has proven to be a useful tool for combining specific attributes from one species, for example disease resistance or cold hardiness, with growth attributes of another species (Fowler 1978). Some studies have shown that the cross of slash pine (*Pinus elliottii* Engelman var. *elliottii*) and loblolly pine (*P. taeda* L.) has at least some potential value ((Barnes and Mullin 1978). Even though loblolly and slash pine have similar environmental requirements, each species has adaptative and morphological attributes which make it more suitable than the other in certain circumstances. Slash pine is more tolerant to poor soil drainage and tip moth damage than loblolly, while loblolly pine is more tolerant to fusiform rust and responds better to intensive management (Powers *et al.* 1975; Barnes and Mullin 1978; Hood *et al.* 1985; Colbert *et al.* 1990).

Slash pine (PEE) has been used successfully to produce hybrids with its subtropical relatives: *P. caribaea* Morelet var. *hondurensis* Barret *et.* Golfari (PCH) and *P. caribaea* Morelet var. *bahamensis* Barret *et.* Golfari (PCB) (van der Sijde and Roelofsen 1986; Nikles 1991; Rockwood and Nikles 1996). Studies in Australia have shown that the F1 PEE x PCH hybrid was always superior in volume production to PEE and at least equal in stem straightness and windfirmness on both well-drained and poorly-drained soils (Nikles and Robinson 1988). On the other hand, PEE x PCB hybrids have not been tested extensively and PCB appears more cold hardy than PCH (Luckhoff 1964; Nikles 1966; Duncan *et al.* 1996). Duncan *et al.* (1996) in a greenhouse study found that PEE was considerably more cold hardy than either slash x Caribbean hybrids, but these taxa have never been tested in the field where plants could suffer several adverse conditions including freeze and pest damage. Furthermore, in order to be commercially important in the Lower Coastal Plain of the southeastern USA, these hybrids have to be tested against improved materials of slash pine and loblolly pine.

The excellent performance of PEE x PCH in other parts of the world motivated the Cooperative Forest Genetics Research Program (CFGRP) to begin a study to assess the potential of this and other hybrids in the Lower Coastal Plain. Seasonal freezing temperatures may be the most significant factor limiting potential utility of hybrids with PCH and PCB in the southeastern USA. given that Caribbean pines occur naturally in frost-free zones and are sensitive to sub-freezing temperatures. Hybridization with slash pine could improve the resistance to cold temperatures (Duncan *et al.* 1996), and perhaps at the same time improve pest and disease resistance.

The primary goals of this chapter are to: 1) Compare survival, cold damage, fusiform rust incidence and third-year height growth, of seven taxa including four slash pine hybrids [slash x loblolly, slash x *P. caribaea* var. *hondurensis*, slash x *P. caribaea* var. *bahamensis*, and the backcross slash x (slash x *P. caribaea* var. *hondurensis*)] against improved and unimproved slash pine and improved loblolly pine; 2) Assess levels of hybrid vigor for cold damage, fusiform rust resistance and height; 3) Determine if intensive management (including fertilization, weed control and tip moth control) changes taxon ranks or hybrid vigor; and 4) Determine the amounts of among family and within-family variability in the hybrids relative to the pure native species.

Materials and Methods

Taxa

Seven different pine taxa are being tested in 11 field sites locations in the Lower Coastal Plain of the southeastern USA (see Chapter 2 and Appendix 2). In eight out of 11 sites, the cooperators of the CFGRP planted all seven taxa: three slash x *P. caribaea* hybrids; slash x loblolly (PEE x PTA), improved slash, unimproved slash and improved loblolly (Table 4-1). Data from these eight sites were used in this chapter for analysis (Series 1, 2 and 3 in Table 2-1).

Table 4-1. Male and female parents that were used to create the seven pine taxa in the experiment. The taxon designation is given in parentheses and the hybrids' designation is given in the body of the table.

Male Parents	Female Parents		
	Improved Slash (30 clones)	Unimproved Slash (17 clones)	Improved Loblolly (17 clones)
P. caribaea var. *hondurensis* (PCH) pollen mix of 30 clones	PEE x PCH		
PEE x PCH (F1H) pollen mix of 25 clones	PEE x F1H		
P. caribaea var. *bahamensis* (PCB) pollen mix of 24 clones	PEE x PCB		
Loblolly (PTA) pollen mix of 30 clones	PEE x PTA		
Orchard pollen of female species	PEE	PEU	PTA

Thirty superior slash pine clones from the CFGRP were used as female parents for all hybrid combinations. Each slash parent was control pollinated with four different pollen mixes: 1) a 30-parent polymix of *P. caribaea* var. *hondurensis* (PCH) to produce the PEE x PCH; 2) a 25-parent polymix of the hybrid PEE x PCH (called F1H) to create the PEE x F1H backcross; 3) a 24-parent polymix of *P. caribaea* var. *bahamensis* (PCB) to produce the PEE x PCB; and 4) a 30-parent polymix of superior clones of *P. taeda* to make the PEE x PTA. All three sources of Caribbean pine pollen were obtained from the Queensland Forest Service in Australia. The loblolly pine pollen was obtained mainly from Atlantic Coastal Plain sources owned by the cooperators of the CFGRP and the NCSU Industry Tree Improvement Cooperative.

Eighteen out of the 30 PEE clones used to produce the hybrid families were the female parents of the improved slash taxon. Thus, the improved slash taxon (PEE) consisted of open-pollinated seed from 18 slash pine clones which are outstanding for volume growth or disease resistance. The PEE seedlot was estimated to have means of 18.3% for volume gain and 37.1% for rust (R50), as predicted by the CFGRP (Appendix 1 and Chapter 3). The 18.3% gain is expressed for 15-year volume above unimproved material. A R50 value lower than 50% indicates resistance to fusiform rust (White *et al.* 1988) and specifically indicates that 37.1% of the seedlings would be rust infected when unimproved seedlings have 50% of rust incidence. The PEE seed came from 11 seed orchards in SE USA.

The unimproved slash pine families (PEU) consisted of open-pollinated seed from 17 parents representative of slash pine as it existed in 1955, before domestication. The PEU seed came from 9 seed orchards in SE USA. For comparison, the PEU seedlot was estimated to have 4.9 % volume gain and an R50 of 51.3%. The improved loblolly taxon (PTA) consisted of open-pollinated seed from 17 of the 30 best available parents (the same 30 clones used in the pollen mix to produce PEE x PTA). Details are not available on breeding values of these parents.

Sixteen families in each taxon were planted per location, but, 18 PEE, 17 PTA, 17 PEU, 19 PEE x PTA, 20 PEE x F1H, 18 PEE x PCH and 17 PEE x PCB families were represented in these 8 tests. Across all sites and taxa, seven PEE mother trees were consistent across all hybrid crosses and in the PEE taxon.

Some of the 30 hybrid crosses did not yield sufficient seed or seedlings for planting as a single family in all sites as initially designed. Thus, for the hybrids PEE x PCH and PEE x PCB only three sites have 16 "single" families. For five more sites, six bulks of PEE x PCH families were formed using two or three families of this hybrid cross. For the same reason, five bulks of two to four PEE x PCB families were created and planted in these five sites (Appendix 8).

Nursery Phase and Field Implementation

Pollination for all hybrids was conducted in February of 1991 and 1992, with subsequent seed collection in 1992 and 1993. Open-pollinated seeds of PEE, PEU and PTA were collected in 1992. Both years' seed harvests were combined, cleaned and cold-stored at 5 °C. In early June 1993, seed of PEE, PEU, PTA and PEE x PTA were disinfected with 10 % hydrogen peroxide, placed in polybags filled with deionized water, imbibed for 24 hours at 25°C, and cold stratified at 5°C for 14 days (Bonner *et al.* 1974). Seed of PEE x F1H, PEE x PCH, and PEE x PCB were disinfected with a 5 % hydrogen peroxide solution and cold stratified at 5°C for 12 days. Germination was done in greenhouse conditions, and plants were moved outdoors after transplanting and seedling establishment. Seedlings were of different sizes at outplanting. Three seedling growers were used to supply the seedlings, and each grower produced the plants to use in two or three test sites (Table 2-1). Each group of two or three test locations that shared the same grower is denoted as a series.

All of the eight field test locations were planted in December 1994 in the Lower Costal Plain, which includes north Florida and the most southerly portions of Georgia (Series 1, 2 and 3 in Table 2-1 and Appendix 2). These sites covered a wide range of soil groups, from well to poorly drained and site indices from 17 to 20 (meters at a base age of 25 years).

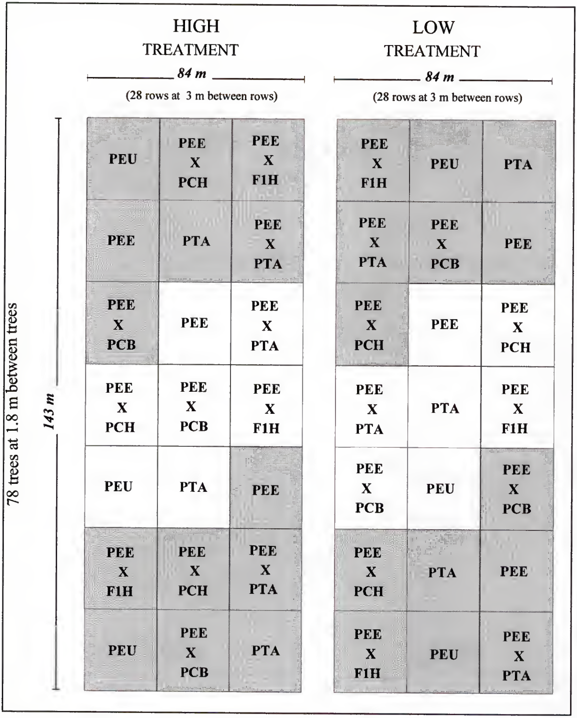
At each location, the field design consisted of a Randomized Complete Block, nested split-plot design, with two cultural treatment levels labeled as High (intensive) and Low (less intensive).Cultural treatments were fully described in Chapter 2. Within each treatment there were 3 complete blocks and a total of 21 taxon plots (7 taxa x 3 blocks; Figure 4-1). Each taxon whole-plot consisted of 16 families with 5 trees per family row (80 trees). All together 3360 trees were planted at each site (2 treatments x 3 blocks x 7 taxa x 16 families x 5 trees/family). Tree spacing varied by location from 1.5 x 3.0 m to 1.8 x 3.0 m.

There is a separation of 21 m or more between High and Low management treatments at each of the 8 sites to mitigate the effects of fertilizer and insecticide applications. Additionally two to four border rows of trees were planted to completely surround the three blocks of each treatment.

Variables Measured

The following variables were measured at all eight sites:

1. Survival was assessed at 1, 1.4, 2, 2.4, and 3 years of age and scored as a binary trait: 0



HIGH TREATMENT

84 m

(28 rows at 3 m between rows)

LOW TREATMENT

84 m

(28 rows at 3 m between rows)

143 m

78 trees at 1.8 m between trees

PEU	PEE X PCH	PEE X F1H
PEE	PTA	PEE X PTA
PEE X PCB	PEE	PEE X PTA
PEE X PCH	PEE X PCB	PEE X F1H
PEU	PTA	PEE
PEE X F1H	PEE X PCH	PEE X PTA
PEU	PEE X PCB	PTA

PEE X F1H	PEU	PTA
PEE X PTA	PEE X PCB	PEE
PEE X PCH	PEE	PEE X PCH
PEE X PTA	PTA	PEE X F1H
PEE X PCB	PEU	PEE X PCB
PEE X PCH	PTA	PEE
PEE X F1H	PEU	PEE X PTA

Figure 4-1. Example randomization of one field location showing 2 treatments, 3 blocks and 7 taxa. Each taxon plot contains 16 families with 5-trees per family row plot, a total of 80 trees (10 trees in 8 rows). Spacing varied from 1.5 to 1.8 m within rows and was 3 m between rows. There are 3360 experimental trees per site, not counting two rows of border trees completely surrounding the three blocks of each treatment.

(dead) and 1 (alive).

2. Cold damage was assessed in the early springs of 1996 (1.4 years) and 1997 (2.4 years), and scored as: 0 = no damage, 1 = slight cold damage (less than 25% of the foliage with damage), 2 = severe cold damage (more than 25% of the foliage with damage), 3 = death from cold.

3. Rust incidence was assessed in the winter of 1997-98 (year 3) and scored as 0 (absence of rust) and 1 (presence of rust); and

4. Height was assessed at age 3 years in the winter of 1997-98, and was measured as height of the highest bud.

Statistical Analysis

Data editing

Data from all eight sites were used for rust, cold damage and survival analyses. One site was eliminated from the height analyses due to extensive deer damage, which resulted in an extremely large mean square error (MSE). For all analyses raw, untransformed data were used because MSEs appeared similar across sites and treatments, and MSE did not increase as the mean increased for any trait. Similar analysis in Chapter 2 showed that both standardized data and raw data produced similar results.

Taxon comparisons and hybrid vigor

A series of analyses of variance (ANOVAs) were performed by pooling data across sites and treatments to examine main effects and interactions of all taxa except PEU. This taxon was not included, because no female PEU clone was included in the hybrid crosses.

Thus hybrid performance must be compared against improved slash pine and improved loblolly pine. The pooled analyses for rust, cold damage and survival were based on individual data (0, 1 observations) using the following linear model:

$$Y_{tijkmn} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + b\tau_{tijk} + f_{m(k)} + sf_{tm(k)} + \alpha f_{im(k)} + s\alpha f_{tim(k)} + e_{tijkmn} \quad (4\text{-}1)$$

where: Y_{tijkm} is the nth observation on a tree observation of the mth familyof the kth taxon in the jth block in the ith treatment at the tth site,

μ is the population mean,

s_t is the random variable for site ~*NID* $(0, \sigma^2_s)$,

α_i is the fixed effect for treatment (High and Low),

$s\alpha_{ti}$ is the random interaction site by treatment ~*NID* $(0, \sigma^2_{s\alpha})$,

$b_{j(ti)}$ is the random variable for block within site by treatment ~ *NID* $(0, \sigma^2_b)$,

τ_k is the fixed effect for taxon (PEE, PTA, PEExPTA, PEExF1H, PEExPCH or PEExPCB),

$s\tau_{tk}$ is the random interaction site by taxon ~*NID* $(0, \sigma^2_{s\tau})$,

$\alpha\tau_{ik}$ is the fixed effect for the interaction treatment by taxon,

$s\alpha\tau_{tik}$ is the random three way interaction site by treatment by taxon ~ *NID* $(0, \sigma^2_{s\alpha\tau})$,

$b\tau_{tijk}$ is the random interaction block(site by treatment) by taxon ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$,

$sf_{tm(k)}$ is the random interaction site by family within taxon ~*NID* $(0, \sigma^2_{fs})$,

$\alpha f_{im(k)}$ is the random interaction treatment by family within taxon ~*NID* $(0, \sigma^2_{f\alpha})$,

$s\alpha f_{tim(k)}$ is the random three way interaction site by treatment by family within taxon ~ *NID* $(0, \sigma^2_{s\alpha f})$,

e_{tijkmn} is the error term ~*NID* $(0, \sigma^2_e)$;

where t= 1,...8 sites; i = 1,2 cultural treatments; j= 1,2,3 blocks per treatment; k= 1,...6 taxa; m=1,...20 families per taxon; and n= 1, ...5 trees.

Analyses for survival were performed separately for each date of assessment (5 dates). Also the number of trees that died from cold, rust or other causes was obtained to explain mortality for some taxa. A pooled analysis for rust was done with data from the six sites that had more than 15% mean rust incidence in both treatments. The other two sites were not considered, because they had very low rust incidence levels (White and Hodge 1987). Nevertheless, rust data from all the eight sites were used to obtain the least square means of rust incidence for all taxa across sites. PEU was included in the latter analysis ranking the incidence means for site-treatment-taxon combination. Thus, PEU was used as baseline in regression analysis to get the infection of all other taxa relative to PEU.

Preliminary analyses for height with model (4-1), demonstrated that variances were different between pure and hybrid taxa. Therefore, to avoid unequal variances among taxa, the whole-plot means (i.e., the mean of 80 trees =16 families x 5 trees if all trees living) were obtained to test height differences across sites and treatments. Heights of all trees and rust-free trees were used to compare taxa with the following model:

$$Y_{tijk} = \mu + s_t + \alpha_i + s\alpha_{ti} + b_{j(ti)} + \tau_k + s\tau_{tk} + \alpha\tau_{ik} + s\alpha\tau_{tik} + e_{tijk} \qquad (4\text{-}2)$$

where Y_{tijk} is the mean of the 80 trees (if living) of the kth taxon in the jth block in the ith treatment at the tth site and t=1,...7 sites; i = 1,2 management treatments; j= 1,2,3 blocks; k= 1,...6 taxa for a total of 252 observations. All other effects are as described in model (4-1).

Moreover, since the standard deviation values for height were increasing as site means increased, an ANOVA was performed to test taxon differences for the coefficient of variation (CV). So, the CV for third-year height was obtained for every five-tree row plot with PROC MEANS (SAS Institute 1988) and used in an ANOVA (model 4-1) to test whether within family variance differed among taxa. Only heights from rust-free trees were used in the analysis.This analysis employed row plot CVs as the unit of observation, so in model (4-1) the subscript "n" is excluded and the block by family effect is part of the error.

For all analyses, PROC GLM was used to test the significance of random effects (SAS Institute 1988). Significance levels and estimated means (using LSMEANS option) for fixed effects (treatment, taxon, treatment by taxon) were obtained from PROC MIXED with the Satterthwaite option (Littell *et al.* 1996). A default probability value of 0.05 was established to show significance unless otherwise specified.

To better understand taxon differences, several single degree-of-freedom contrasts were computed. Specific null hypotheses for contrasts were: 1) There are no differences between two taxa such as between PEE and any hybrid; 2) There are no differences between PEE x PTA and the average performance of PEE and PTA; and 3) There are no differences between PEE x F1H and the average performance of PEE and PEE x PCH. The last two contrasts were performed to determine whether or not hybrid vigor was expressed in the hybrid taxon for all traits measured. Those contrasts were calculated based on:

$$\text{Hybrid vigor} = H/((P_1 + P_2)/2) \tag{4-3}$$

Thus, the single degree-of-freedom compared each hybrid mean (H) to the mean of the two parental taxa (P_1 and P_2). A significant contrast indicated that H was not linearly intermediate to P_1 and P_2, and was taken as evidence of hybrid vigor.

Frequency polygons for height growth using only healthy trees were constructed to compare height distributions of different taxa across sites. All observations were adjusted by the height means for sites and blocks and then the height deviations were pooled across sites to form a single polygon for each taxon. Normality was tested with Shapiro-Wilk tests in PROC UNIVARIATE (SAS Institute 1990). Also, to test whether median values were different from means, the hypothesis "Median-mean = 0" was tested by a T-test in PROC UNIVARIATE. To test differences in height medians among taxa, a Brown-Mood test (Steel and Torrie 1980 p.543) was performed using PROC NPAR1WAY with the median option (SAS Institute 1988).

Heritabilities

Heritabilities (h^2) for third-year height growth were estimated separately for both treatments and each taxon using the individual tree data pooled across sites. To remove the effects of scale, height was standardized by dividing each observation in a site-treatment-block combination by the corresponding square root of the phenotypic variance for that block (Visscher *et al.* 1991; Hodge *et al.* 1996). The goal in h^2 estimation was to determine the variance among families in the hybrids relative to that in slash pine and loblolly pine.

Variance components were estimated by PROC MIXED with the restricted maximum likelihood method, REML (Littell *et al.* 1996). Analyses of variance were performed for each treatment and taxon combination (2 treatments x 6 taxa = 12 analyses) to estimate the significance of family, site by family, treatment by family, and block by family interaction. The model was obtained by dropping the taxon effect from model (4-1) (i.e., dropping all terms with subscript *k*). The model for each treatment-taxon combination was the following:

$$Y_{tjmn} = \mu + s_t + b_{jt} + f_m + sf_{tm} + bf_{tjm} + e_{tjmn} \qquad (4\text{-}4)$$

where: Y_{tjmn} is the n^th observation of the m^th family in the j^th block at the t^th site; and t=1,...10 sites; j= 1,2,3 blocks; m= 1,...20 families; and n=5 trees. All other effects are as described in model (4-1), but site and block where considered as fixed effects.

The open-pollinated families in the PEE and PTA taxa were assumed to be half-sib families; hence the variance component for families (σ^2_f) can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A) (Falconer and Mackay 1996).

Individual tree heritabilities were estimated as:

$$h^2 \text{ or } h^2_h = 4^* \sigma^2_f \; / \; \sigma^2_f + \sigma^2_p + \sigma^2_w \qquad (4\text{-}5)$$

For the hybrids, a hybrid heritability (h^2_h), was calculated as the ratio of 4 times the hybrid family variance ($4^*\sigma^2_{fh}$) over the total phenotypic variance, also using Equation (4-5). These h^2_h values for hybrids may be larger than for pure species, because in the hybrids additive and non-additive variance are confounded in σ^2_{fh} and gene frequencies in parental species may be different (Cockerham 1961; Wei *et al.* 1991). In any case, the h^2_h ratio can be interpreted as the proportion of variation in the hybrid population that is attributable to genetic differences among hybrid families, and useful for selection.

Estimates of heritability were obtained in three ways with 1) heights of all trees, 2) only healthy trees and 3) without dwarf trees. A dwarf tree was defined as any tree smaller than 3 standard deviations from the height mean in each cultural treatment. For PEE x PXH and PEE x PCB bulked lots were excluded from these analyses.

Results and Discussion

Survival and Cold Hardiness

Significant differences ($p < 0.001$) for mean survival existed among the six taxa in all five measurement periods (from one year to three years after planting). Treatment and treatment by taxon interaction effects were not significant for any measurement (Table 4-2). Results were similar for mortality due to cold temperatures, with highly significant taxon differences ($p<0.001$).

The PEE x PCH hybrid was the most susceptible to low temperatures, and had the lowest survival percentage at all five survival measurements (Figure 4-2). At three years of age, PEE x PCH survival was 68% averaged across all sites (ranging from 49 to 83% at individual sites); its lower survival was partially caused by its low cold resistance, since 14.7% of the PEE x PCH trees were killed by freezing temperatures (Appendix 9). Evaluation at 16 months (1.4 years) showed an average of 14% of the trees in this taxon were

Table 4-2. Analysis of third-year data pooled across sites and cultural levels for survival and rust incidence.

Source	SURVIVAL[a]			RUST INCIDENCE[b]		
	DF	F value	Pr > F	DF	F value	Pr > F
SITE	7	2.87	0.0256	5	12.71	0.0045
TREATMENT (H *vs.* L)	1	0.45	N.S.	1	0.10	N.S.
SITE*TREATMENT	7	1.31	N.S.	5	5.02	0.0081
TAXON	5	21.80	0.0001	5	22.12	0.0001
[c]Hybrid Vigor in PEE x PTA hybrid	1	41.98	0.0001	1	1.14	N.S.
[d]Hybrid Vigor in PEE x F1H hybrid	1	5.46	0.0220	1	3.77	0.0548
PEE *vs.* PEE x PCH	1	62.70	0.0001	1	8.47	0.0044
PEE *vs.* PEE x PCB	1	3.42	0.0683	1	23.21	0.0001
PEE x PCH *vs.* PEE x PCB	1	38.55	0.0001	1	3.78	0.0508
SITE*TAXON	35	3.07	0.0001	25	1.30	N.S.
TREATMENT*TAXON	5	0.62	N.S.	5	0.22	N.S.
SITE*TREAT*TAXON	35	1.51	0.0460	25	1.08	N.S.
FAMILY(TAXON)	112	6.84	0.0001	112	8.38	0.0001
SITE*FAMILY(TAXON)	606	1.51	0.0001	428	1.05	N.S.
TREAT*FAMILY(TAXON)	112	0.95	N.S.	112	0.87	N.S.
SITE*TREAT*FAMILY	604	1.07	N.S.	425	1.21	0.0026
ERROR	21102			14066		

a. ANOVAs from measurements at 1, 1.4, 2, and 2.4 years showed similar results as at 3 years of age.

b. ANOVA for rust was for the six sites with more than 15% of rust incidence.

c. Hybrid vigor of the PEE x PTA hybrid was analyzed by: PEExPTA / (0.5 PEE+ 0.5 PTA).

d. Hybrid vigor of the PEE x F1H backcross hybrid was analyzed by:
PEE x F1H / (0.5 PEE + 0.5 PEE x PCH).

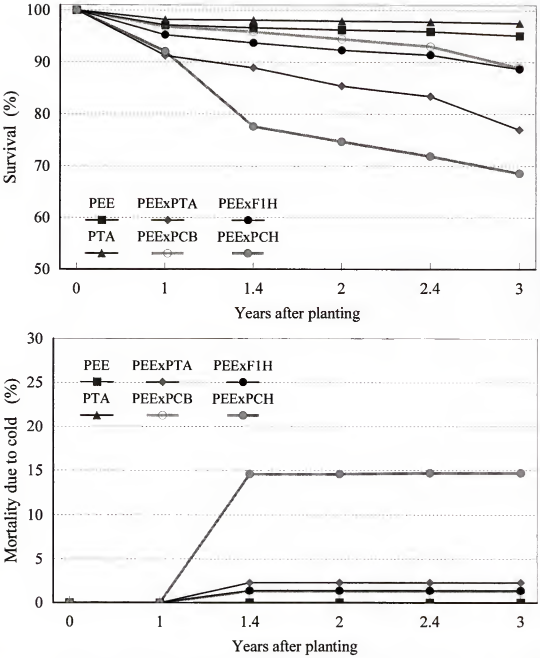


Figure 4-2. Total cumulative survival and cumulative mortality due to cold (in percentage) for the pure slash (PEE), loblolly pine (PTA) and the hybrids slash x loblolly pine (PEE x PTA), slash x *caribaea* var. *bahamensis* (PEE x PCB), slash x *caribaea* var. *hondurensis* (PEE x PCH) and the backcross slash x PEE x PCH (PEE x F1H). Evaluations at 1, 2, and 3 years of age were performed in January 1996-1998. Evaluations at 1.4 and 2.4 were done in May-1996 and May-1997, respectively. ANOVA's showed that significant differences ($p<0.05$) existed among the 6 taxa at evaluations 1.4 through 3 years-old in both traits. Cultural treatments were not significant different at any age, so averages are combined across both treatments.

killed by the cold temperatures during the winter 1995-96. Meteorological data indicated that this particular winter had more days with freezing temperatures than others in this period.

The PEE x F1H backcross hybrid was more similar to PEE for survival, cold damage, and number of dead trees from cold than to the PEE x PCH hybrid (the other parental species of this hybrid taxon). Thus, backcrossing the PEE x PCH hybrid to PEE, a more cold resistant parent, was effective in increasing cold hardiness and survival in that taxon. Duncan *et al.* (1996), studying similar hybrids as young seedlings under control chamber conditions found that the hybrid PEE x PCH was more comparable to the more freeze susceptible parent, PCH. This study showed that the hybrid PEE x F1H was more similar to the most cold resistant parent, PEE.

PEE x PCB was more cold hard than PEE x PCH. Duncan *et al.* (1996) also found that PEE x PCB was more cold hard than PEE x PCH. In fact, this was expected since the *bahamensis* variety inhabits colder areas than *hondurensis* (Nikles 1966). Mean values of cold damage and survival indicated that PEE x F1H was as cold resistant as PEE x PCB, but both hybrids had somewhat more cold damage than and with the same survival as pure slash.

PEE x PTA had significantly lower survival than both parental species (and also than PEE x F1H and PEE x PCB). Further, single-degree contrasts indicated a negative hybrid vigor for survival (Table 4-2, Appendix 9). The generally lower survival of PEE x PTA seems associated with the large variability for vigor among trees in this taxon. Some hybrid trees were small trees and tended to be very susceptible to cold temperatures, rust or other causes.

Third-Year Rust Infection

The pooled analysis showed no significant differences between cultural treatments for average rust incidence. No rank changes were detected due to site-by-taxon or treatment-by-taxon interactions in the pooled analysis, but highly significant taxon differences existed (Table 4-2). The slash x Caribbean hybrids had a higher infection rate for fusiform rust than pure slash pine or loblolly pine (Figure 4-3). Overall, as was noted in Chapter 2, PEE had nearly twice the rust infection of PTA. Rust incidence coefficients from the regression analysis based on the rust incidence of unimproved slash pine (PEU), indicated that both the PEE x PCH and PEE x F1H hybrids were more rust resistant than PEU, but PEE x PCB was as susceptible as unimproved slash pine (Figure 4-3). The PEE x PCH hybrid had less rust incidence than PEE x PCB, although the single-degree contrast was only slightly significant ($p<0.051$). Tainter and Anderson (1993) screening a sample of commercial seed found that *P. caribaea* var. *hondurensis* seedlings were very susceptible to fusiform rust. In fact, all varieties of *P. caribaea* were at least somewhat susceptible to fusiform rust compared with rust resistant slash pine (Jewel 1960; Tainter and Anderson 1993; Doudrick *et al.* 1996).

Negative hybrid vigor was detected when comparing the PEE x F1H backcross hybrid to the average rust incidence of its parental species, PEE and PEE x PCH hybrid. In fact, the var. *hondurensis* backcross to PEE was as rust susceptible as PEE x PCH. The pollen mixed from PEE x PCH used to create the PEE x F1H was obtained from the Queensland Forest Service in Australia. This pollen, most likely, is the product of slash pines that have not been improved for fusiform rust resistance, since this pest is not present in Australia. So, it is likely that the F1H pollen was unimproved for rust resistance. In fact, two

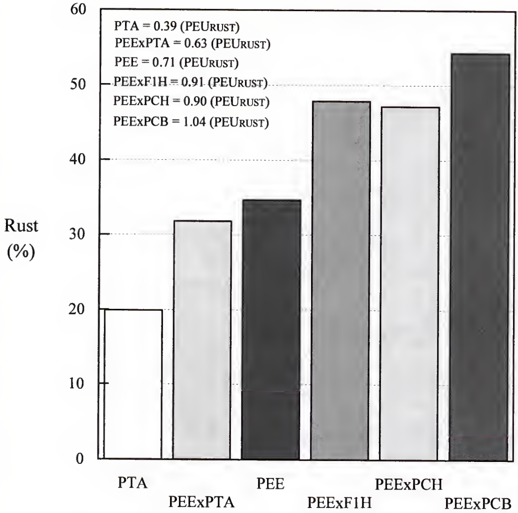


Figure 4-3. Mean cumulative rust incidence at three years of age by taxa for pure loblolly pine (PTA), pure slash pine (PEE) and the hybrids: PEE x PTA, slash x *caribaea* var. *hondurensis* (PEE x PCH), slash x PEE x PCH (PEE x F1H), and slash x *caribaea* var. *bahamensis* (PEE x PCB). Treatment effects and interactions with other independent variables were non significant, so averages are combined across both treatments and sites. Rust incidence coefficients based on unimproved slash pine (PEU) were obtained by regression of each taxon's rust against PEU. For the full model y= PEURUST + PEURUST*TAXON, $R^2 = 0.92$. Taxon differences are highly significant and specific contrasts are presented in Table 4-2.

other tests in northeastern Florida indicated, that the PEE x PCH hybrid formed in Australia was taller than PEE but very rust susceptible at three years of age (Rockwood and Nikles 1996).

The single-degree contrast of hybrid vigor for the six sites with more than 15% rust incidence indicated that the PEE x PTA hybrid was intermediate for infection rate between the parental species. However, across all sites rust associated mortality at three years of age in this hybrid was four times greater than slash pine (Appendix 9). Furthermore, when rust incidence was averaged across all 8 sites, the mean rust incidence of PEE x PTA was closer to slash pine, the susceptible parental species (Figure 4-3). Testing few crosses, Schmitt (1968) found that the hybrid PEE x PTA was more susceptible to fusiform rust than both pure slash and loblolly pine. This was not the case here, but there was some indication that the hybrid PEE x PTA was more similar to the rust susceptible parent, PEE.

Third-Year Height

Taxon comparisons

The pooled analysis using data only from healthy trees showed that the intensive culture had effectively increased third-year height ($p=0.0029$ in Table 4-3). No rank changes were detected due to site by treatment interaction since all taxa were taller in the intensive treatment at all sites. In spite of the significant interactions of site by taxon and treatment by taxon ($p<0.01$), no important taxon rank changes were found across sites (data not shown) nor across treatments (Figure 4-4). Highly significant taxon differences were found in both treatments, and differences among taxa increased in the high treatment. Improved loblolly

Table 4-3. Analysis of variance for third-year height. Data were pooled across seven sites and two cultural levels. Values were analyzed based on whole-plot means of healthy trees (252 observations = 7 sites x 2 treatments x 3 blocks x 6 taxa). Contrasts below the line are specific to high and low cultural treatment.

Source	DF	F value	Pr > F
SITE	6	2.49	N.S.
TREATMENT (H *vs.* L)	1	23.45	0.0029
SITE*TREATMENT	6	16.27	0.0001
TAXON	5	16.38	0.0001
[a] Hybrid Vigor in PEE x PTA hybrid	1	27.60	0.0001
[b] Hybrid Vigor in PEE x F1H hybrid	1	3.85	0.0590
PEE *vs.* PEE x PCH	1	11.99	0.0016
PEE *vs.* PEE x PCB	1	0.07	N.S.
PEE x PCH *vs.* PEE x PCB	1	11.77	0.0018
SITE*TAXON	30	2.81	0.0030
TREATMENT*TAXON	5	5.60	0.0009
HIGH Hybrid Vigor in PEE x PTA hybrid	1	36.88	0.0001
Hybrid Vigor in PEE x F1H hybrid	1	3.57	0.0648
PEE *vs.* PEE x PCH	1	17.84	0.0001
PEE *vs.* PEE x PCB	1	0.69	N.S.
PEE x PCH *vs.* PEE x PCB	1	11.52	0.0014
LOW Hybrid Vigor in PEE x PTA hybrid	1	8.70	0.0049
Hybrid Vigor in PEE x F1H hybrid	1	5.35	0.0252
PEE *vs.* PEE x PCH	1	2.97	0.0910
PEE *vs.* PEE x PCB	1	0.60	N.S.
PEE x PCH *vs.* PEE x PCB	1	6.24	0.0159
SITE*TREAT*TAXON	30	1.01	N.S.

a, b. Definition of contrasts are in Table 4-2. Degree of freedom for error is 140.

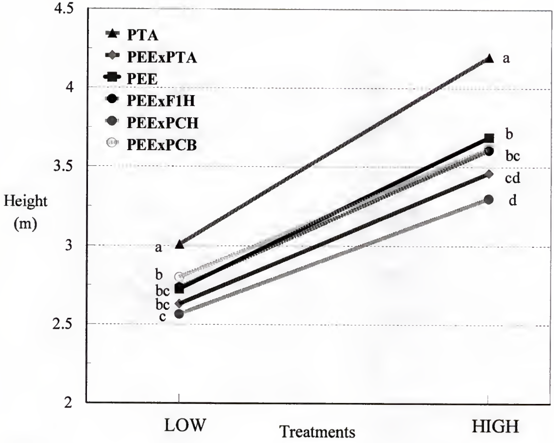


Figure 4-4. Third-year height by taxon in the two treatments across seven sites. The height values include only healthy trees. Mean height values using all trees were smaller, but very similar to those presented. Treatment and taxon differences were highly significant and some specific contrasts are presented in Table 4-4. The treatment by taxon interaction was significant ($p<0.05$). Taxon means with same letter are not significantly different within a treatment at $p=0.05$.

pine was the tallest taxon at three-years of age and was most responsive to the high cultural treatment.

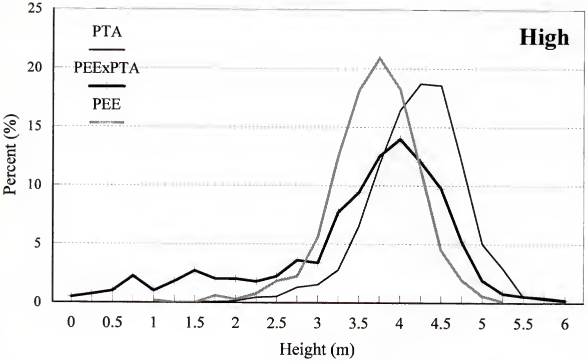
Similar results were found when pooled analyses were done including all trees (healthy and diseased trees), but means were somewhat smaller when diseased trees were included. On average, native taxa were shorter by 1%, while the slash x Caribbean hybrids were shorter by 5% when fusiform rust infected trees were included. However, no taxon rank changes were noticed when comparing analyses employing only healthy trees to those including both healthy and diseased trees.

Positive hybrid vigor was detected for height in both treatments when comparing the PEE x F1H backcross hybrid to the average third-year height of the parental species PEE and PEE x PCH. The backcross taxon was not significantly different from slash pine. Its faster growth relative to PEE x PCH may be partially due to the increased cold hardiness conferred by the backcross to PEE. In fact, PEE x PCH was the shortest taxon of all. PEE x PCB was taller than PEE x PCH in both treatments ($p<0.02$). This difference was also significant when including healthy and diseased trees in the ANOVA. The early advantage of PEE x PCB may be due to its superior cold hardiness.

The hybrid PEE x PTA was the second shortest taxon, and negative hybrid vigor was detected for height growth in both treatments. In the low treatment, the PEE x PTA was not different from PEE, but with intensive culture, PEE was taller than PEE x PTA ($p<0.02$). Barnes and Mullin (1978) testing the PEE x PTA hybrid and both parental species in South Africa found that hybrid vigor was positive where environmental conditions were marginal for both slash and loblolly pine and negative where environmental conditions were favorable for the two parental species. This may be the case for slash pine and loblolly pine growing in the Lower Costal Plain of USA where conditions are favorable for both parental species.

The frequency polygon for heights of the PEE x PTA hybrid revealed a skewed distribution to the left, meaning that many trees were very short (Figure 4-5). In the high treatment, PEE x PTA heights were somewhat outside of a normal distribution ($W=0.8962$, where values lower than 0.90 may lead to rejection of the hypothesis of normality, SAS Institute 1990). While PEE x PTA heights were close to a normal distribution in the low treatment ($W=0.9416$). The greater frequency of very small trees reduced the mean height of the PEE x PTA hybrid. Median values for PEE x PTA were somewhat higher than for PEE (Table 4-4). The median is not as influenced by extreme values as is the mean (Daniel 1974), allowing a better comparison of these taxa. The PEE x PTA median was higher than its mean in both treatments ($p<0.01$), due to its skewed distribution. Thus, when median values were compared in the high treatment, the PEE x PTA hybrid was taller ($p<0.05$) than PEE. Similarly, the mode of the hybrid population was located between the two parental taxa in the high treatment, and closer to the taller taxon (PTA) in the low treatment (Figure 4-5).

If a dwarf tree is defined as any tree smaller than three standard deviations from the mean of all three taxa, then 5% of the PEE x PTA trees may be classified as dwarves while 0.17% of the PEE and 0.14% of the PTA were dwarves in the low treatment. Further, 8% of the PEE x PTA, 0.20% of the PEE and 0% of the PTA trees were dwarf trees in the high treatment. Schmitt (1969) found that the combination of foreign genomes in slash x shortleaf pine hybrids is apparently conducive to mixoploidy or polyploidy which may produce dwarf trees (Schmitt and Snyder 1971). Saylor and Smith (1966) found also higher chromosomal



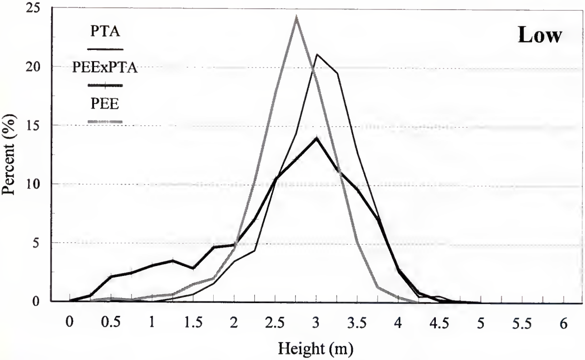


Figure 4-5. Frequency polygons of third-year height for the improved slash (PEE), improved (PTA) and the F1 hybrid (PEE x PTA) by treatment. Frequencies are for all rust-free trees and height values were adjusted by the site and block means of these taxa. Percentage values were obtained by PROC FREQ (SAS 1988) with 24 intervals of 0.25 m.

irregularities in many hybrid combinations of several pine species than in the pure species.

Some very tall PEE x PTA hybrid trees were detected when adjusted by the site and block mean. For example, in the high treatment the tallest 2% of the PEE x PTA trees were taller than any slash pine tree and as tall as the best 4% of the loblolly pine trees. Further, 54% and 52% of the PEE x PTA hybrid trees were taller than the median PEE tree in the high and low treatments, respectively.

Table 4-4. Measurements of central tendency for third-year height growth. Values in meters were obtained for healthy trees and values adjusted by the height means of site and block for PEE, PTA and their F1 hybrid. The mode was obtained from the most frequent interval in Figure 4-5.

TAXON	LOW				HIGH			
	Mean	Mode	Median[a]	S [b] (%)	Mean	Mode	Median	S (%)
PTA	3.02	3.00	3.05* a	70	4.20	4.25	4.25** a	83
PEE x PTA	2.64	3.00	2.81**b	52	3.50	4.00	3.79** b	54
PEE	2.72	2.75	2.75* b	50	3.68	3.75	3.70 c	50
PEE x F1H	2.71	2.75	2.75* b	49	3.62	3.75	3.71 bc	51
PEE x PCH	2.55	2.60	2.60* c	40	3.29	3.37	3.37** d	31
PEE x PCB	2.79	2.75	2.81 b	52	3.66	3.75	3.71 bc	51

a. Height medians were significantly different from the mean with $p<0.05$ * or $p<0.01$** Letters indicate medians among taxa, where taxon medians with same letters are not significant different at $p=0.05$.

b. Superiority (S) was calculated as the percentage of trees in each taxon that were bigger than the median of PEE. Thus, PEE value is 50%.

Frequency polygons were also built for third-year height of PEE and the slash x Caribbean hybrids (Appendix 10). The PEE x F1H and PEE x PCH frequency distributions were quite similar to the PEE distribution. The frequency polygon for PEE x PCH hybrid was somewhat skewed to the left with 1% and 2% of dwarf trees in the low and high treatment, respectively. When comparing the median, mode or superiority values (percentage of trees in each taxon that were bigger than the median of PEE), the hybrids PEE x F1H and PEE x PCB were as tall as PEE (Table 4-4). PEE x PCH had 31% of its trees taller than the PEE median. If this trend continues some individuals from these taxa have potential use in breeding.

Family comparisons

Heritabilities from pooled analyses were calculated for both pure species (PEE and PTA) and the hybrids. Hybrid heritability (h^2_h), calculated as the ratio of 4 times the hybrid family variance (σ^2_{fh}) over the total phenotypic variance, were larger than heritabilities for the pure species (Table 4-5). In general, when estimates were performed on healthy trees, h^2_h values were even higher. Higher heritabilities were estimated in the high treatment, most probably resulting from a reduction in the error variance in the intensive culture as it was found in analyses in Chapter 3. These estimates of h^2 and h^2_h should be taken with caution due to the small number of families and young age.

Table 4-5. Estimates of heritabilities for pure taxa (h^2) and estimates of hybrid heritabilities ($h^2_h=4*\sigma^2_{fh} / \sigma^2_{fh} + \sigma^2_p + \sigma^2_w$) for early height growth in all taxa by treatment. Values were obtained using standardized data in three different analyses: Including all trees, healthy trees and without dwarf trees. For PEE x PCH and PEE x PCB bulked families were not included.

TAXON	h^2 or h^2_h in High Treatment			h^2 or h^2_h in Low Treatment		
	All trees	Healthy trees	Without Dwarfs	All trees	Healthy trees	Without Dwarfs
PTA	0.14	0.14	0.13	0.07	0.08	0.07
PEE x PTA	0.18	0.28	0.13	0.14	0.16	0.08
PEE	0.10	0.15	0.10	0.04	0.16	0.03
PEE x F1H	0.15	0.16	0.14	0.08	0.12	0.05
PEE x PCH	0.19	0.24	0.19	0.37	0.28	0.33
PEE x PCB	0.13	0.23	0.11	0.08	0.13	0.04

Analysis of within-family variance of third-year height

To examine whether taxa differed in variability among trees within the same family, the within-family coefficient of variation (CV) was calculated for each taxon and treatment combination using the third-year height from the five trees of a given family in each row plot. There were 3598 of these plot-level, within-family CVs that were subjected to ANOVA (7 sites x 2 treatments x 6 taxa x 3 blocks x 16 families less missing plots). Less intensive culture (low) had more within-plot variability for height growth than intensive culture (high) when comparing the heights of healthy trees ($p<0.04$, Figure 4-6 and Appendix11). Data analyses in Chapter 3 also demonstrated that intensive culture ameliorated environmental variability.

Taxa also differed markedly in the amount of within-plot variability and the trends were consistent across treatments. The PEE x PTA taxon was the most variable of all taxa. This hybrid had a mean coefficient of variation twice that of both PEE and PTA (Figure 4-6). Growing in South Africa, the slash x loblolly pine hybrid at three years of age had larger phenotypic variance for height growth than the pure species (Barnes and Mullin 1978). In summary, PEE x PTA showed a negative hybrid vigor for height growth (Figure 4-4), but higher variability (Figure 4-6), probably due to high frequencies of both very short and very tall trees (Figure 4-5).

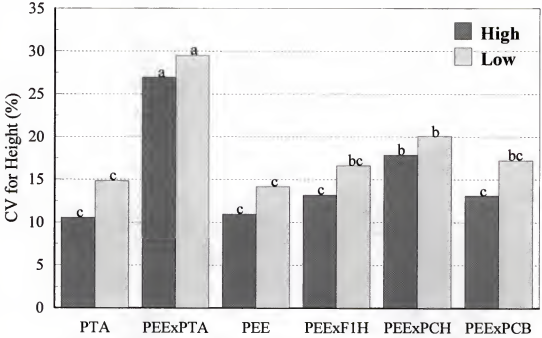


Figure 4-6. Within-plot coefficient of variation (CV) for third-year height in the High and Low treatments for improved loblolly pine (PTA), improved slash pine (PEE) and the hybrids: PEE x PTA, slash x *caribaea* var. *hondurensis* (PEE x PCH), slash x PEExPCH (PEE x F1H), and slash x *caribaea* var. *bahamensis* (PEE x PCB). Data based on rust-free trees. Treatment differences were significant ($p<0.04$), but treatment by taxon interaction was not significant. Taxon differences were highly significant. Taxon means with same letter are not significantly different at $p=0.05$ (from single-degree of freedom contrasts) in each treatment.

In general, the slash x Caribbean hybrids were more variable than pure slash pine in the low treatment. PEE x PCH was the second most variable taxon. This hybrid was significantly more variable than PEE in both treatments. Considerable phenotypic variation among and within families has been found for several traits in PEE x PCH including height growth in Australia (Nikles and Robinson 1988).

General Discussion and Conclusions

In general, results indicated that all hybrid taxa are suffering some problems of adaptation in the Lower Coastal Plain of USA. Overall, height means of the hybrids indicated a lack of positive hybrid vigor. However, very outstanding trees and hybrid families may be found in all of these hybrid taxa, and evaluations at older ages are needed to draw more precise conclusions about their productivity.

On average, the PEE x F1H (the backcross of PEE x PCH to PEE) and the PEE x PCB were better adapted than PEE x PCH at three years of age. Both taxa were less affected by cold damage and taller than PEE x PCH, and had height growth similar to the pure-improved slash pine (PEE) families. Hybridization has proven to improve cold hardiness in other tree species, for example, *P. rigida* Mill. x *P. taeda* hybrids are more cold resistant than pure loblolly pine (Hyun, 1976; Genys, 1988).

All varieties of *P. caribaea* seem relatively susceptible to fusiform rust (Jewel 1960; Tainter and Anderson 1993; Doudrick *et al.* 1996). The var. *bahamensis* seems somewhat more susceptible than the var. *hondurensis*. Likely, *P. caribaea* has evolved in the absence of fusiform rust. No species of *Quercus* suitable as the alternate host of *C. q. fusiform* presently occurs in the Caribbean area (Burns and Honkala 1990), but some *Quercus* species grow in the natural distribution of var. *hondurensis* (Kellman 1976).

Overall, the PEE x PTA hybrid had rust infection similar to the most rust susceptible parent, PEE. The PEE x PTA hybrid taxon had a significant frequency of abnormal trees that reduced the taxon mean values, but median height is significantly superior to PEE in the high treatment. In any case, PEE x PTA was less well adapted than pure loblolly pine.

Fowler (1978) hypothesized that when two species have evolved and adapted to similar local conditions, their hybrid progeny may have some degree of negative hybrid vigor. This may be the case for loblolly pine and slash pine in the LCP, where they are well adapted. Generally, when interspecific hybrids are planted in zones which are marginal for the pure species or as exotic in radically different environments from natural distributions of the parental species, the hybrids tend to show positive hybrid vigor (Martin 1989). For example, in Texas, outside the range of slash pine and in drier environments, the hybrid PTA x PEE (the reciprocal cross) was taller than PTA although with lower survival (Long 1973). In Queensland, Australia, on poorer sites the F1 hybrid PEE x PCH outperforms both pure species, but in better quality sites PCH is as productive as the F1 (Powell and Nikles 1996). Barnes and Mullin (1978) concluded that the slash x loblolly hybrid may be good where the species are grown as exotics and where the F1 progeny are located in "hybrid habitats".

Very tall hybrid families were detected when adjusted by the site and block mean of the native taxa. Using only healthy trees, one PEE x PCB family was better than the best family of PTA and two PEE x PCB families were better than any PEE family in the low treatment. The top 20% of families for height in the low treatment (23 families), were composed of 13 PTA families, 4 PEE x PCB families, 3 PEE x PTA, 2 PEE and 1 PEE x PCH family. Meanwhile, in the high treatment, the composition of the top 20% of the families was 17 PTA families, 2 PEE x PTA, 2 PEE x PCB, 1 was a backcross PEE x F1H, and 1 was a PEE family.

Clearly, there are some tall trees in all hybrid taxa that might be useful in a breeding program. For example, in the high treatment the tallest 2% of the PEE x PTA trees were taller than any slash pine tree and as tall as the best 4% of the loblolly pine trees. In any case, outstanding hybrid trees that are rust free may be found in each taxon. However, rust resistance needs to be improved before considering operational deployment of slash x Caribbean hybrids in areas where rust hazard is high.

The larger hybrid heritabilities (h^2_h) and more within-family variability compared to within families of parental species may be exploited by selection within hybrid families to find outstanding recombinants and increase genetic gain above that projected on the basis of average taxon performance.

Large gains may be obtainable via family and clonal selection of outstanding hybrid trees. Examples of this in pines are PEE x PCH in Queensland, Australia and *P. rigida* x *P. taeda* in Korea, where hybrids are mass propagated by seed (Nikles 1992; Kim and Zsuffa 1994). However, relatively few hybrids in pines have been developed to the stage of operational use, because the major constraint is the difficulty and extra expense of mass producing hybrids, either by seed or vegetatively. In this study, the PEE x F1H and PEE x PTA hybrids produced an average of 32 and 30 seeds per cone (Hodge *et al.* 1993b) which is acceptable for breeding purposes. Further, no seedling production problems were detected for the PEE x F1H and PEE x PTA hybrids.

Hybrid breeding programs are currently operational with several species in the genera *Eucalyptus, Populus* and *Salix* (Zobel 1993, Bisoffi and Gullberg 1996). These programs have been greatly facilitated by the ease of vegetative propagation in the species of these genera. As efficient means of large-scale vegetative propagation become more available with pines (Stelzer *et al.* 1998), breeding for hybrids will almost certainly become more popular. This will allow outstanding individuals to be propagated operationally no matter their genetic composition, and without using extensive controlled pollination.

The technique of reciprocal recurrent selection used to develop commercial F1 varieties does not hold much promise if these early results (showing poorer mean performance of all tested F1 hybrids) are borne out in the future. However, excellent individual trees in several of these taxa would be detected and maybe useful for breeding purposes in hybrid programs that combine genes from the hybrids back with the parental PEE and PTA species to form synthetic backcross taxa in various combinations.

CHAPTER 5
TAXON AND FAMILY LEVEL DIFFERENCES IN TIP-MOTH INFESTATION OF LOBLOLLY PINE, SLASH PINE AND SOME SLASH PINE HYBRIDS

Introduction

Pine tip moths, *Rhyacionia* spp., are major pests of young pines in the eastern United States. During recent years, tip moths have become increasingly abundant and destructive to the establishment of large pine plantations (Yates 1960, *et al.* 1981; Berisford *et al.* 1992). Larvae of pine tip-moth inhabit growing tips of pines, where their feeding habits may produce deformation of the host tree, loss or retardation of growth and reduction of cone crops (Yates 1960; Cade and Hedden 1987; Berisford 1988). In addition, it is thought that tip moths create wounds which may be infected by airbone spores of pitch canker (Blakeslee *et al.* 1980) or fusiform rust (Powers and Stone 1988; Hedden *et al.* 1991).

The two most important commercial timber species in the Southeast, loblolly pine (*P. taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelman), sustain injury by tip moths (Yates 1960, *et al.* 1981; Hood *et al.* 1985; Foltz 1989). Although these insects are present in natural stands, the most severe damage is observed on young pines, especially in even-aged plantations (Lashomb *et al.* 1980; Berisford 1988). Like several other forest tree pests, increased damage from pine tip moth is frequently associated with an increased intensity of forest management (Berisford and Kulman 1967; Hood *et al.* 1988).

Accordingly, greater damage may be expected because of the increasing interest in intensive culture to produce larger volumes of wood per unit area (Hagler 1996).

Two out of the 23 Neartic species of *Rhyacionia* are commonly found in the lower Coastal Plain (LCP) of the southeastern USA (Powell and Miller 1978). It is generally felt that Nantucket tip moth (*R. frustrana* Comstock) prefers loblolly pine, while the Subtropica tip moth (*R. subtropica* Miller) prefers slash pine (Merkel 1963; Yates 1966; McGraw 1975; Hertel and Benjamin 1977; Hood *et al.* 1988). However, no testing to provide further evidence of tip moth's preferences has been conducted in the LCP when improved loblolly and slash pine are growing in the same locations with their F1 hybrid.

Current strategies to control damage from tip moths include the use of more resistant species for planting and the use of insecticides after planting (Lashomb *et al.* 1980; Stephen *et al.* 1982). Loblolly pine is seriously damaged, while slash pine is somewhat resistant (Yates 1960; Berisford 1988). Unfortunately, tests protected by insecticides cannot be used to identify resistance mechanisms and select for resistance to tip moth. In fact, insecticide applications could even lead to the selection of trees that are susceptible to pine moth (Berisford 1988). Holst (1963) concluded that individual tree selection and hybridization would be required to improve resistance in loblolly pine. Some studies have shown that there is variability among provenances of loblolly pine with respect to tip moth resistance (Berisford 1988; Schmitling and Nelson 1996). Also, some family differences in tip moth incidence may be found in loblolly pine (Young *et al.* 1979; Cade and Hedden 1989), but almost no heritability estimates have been reported for tip moth resistance.

The excellent performance of some slash x Caribbean hybrids in other parts of the world motivated the Cooperative Forest Genetics Research Program (CFGRP) to assess the growth potential of three slash x Caribbean hybrids in the LCP. Commercial value in the southeastern USA requires that these hybrids be tolerant to tip moth. Improved loblolly, improved slash and the slash x loblolly pine hybrid was also included in these field trials to allow comparisons of several taxa across 11 sites for the relative resistance to the moth attack.

The main goals of this chapter are to) Obtain information about tip moth resistance among seven taxa planted across eleven sites in the LCP; 2) Assess the effect of hybridization of slash pine and loblolly pine on tip moth resistance; 3) Determine if family differences in resistance could be useful for selection; and 4) Explore the possibility that tip moth preferences and family variability in resistance are useful in understanding mechanisms of resistance to this pest.

Materials and Methods

Taxa

This experiment is a subset of the larger series of field experiments, in which seven different pine taxa were tested: Improved loblolly pine (PTA), improved slash pine (PEE), unimproved slash pine (PEU), the slash x loblolly F1 hybrid (PEE x PTA), and three slash x Caribbean pine hybrids: slash x *P. caribaea* var. *hondurensis* Barret *et.* Golfari (PEE x PCH), slash x *P. caribaea* var. *bahamensis* Barret *et.* Golfari (PEE x PCB) and the backcross of PEE x PCH to PEE (PEE x F1H). Data from tip moth incidence in these taxa, planted in 11 field test locations in LCP (Table 2-1) are analyzed here.

The improved slash taxon consisted of open-pollinated seed from 18 slash pine trees which are outstanding in terms of volume growth or disease resistance. The unimproved slash pine families consisted of open-pollinated seed from 17 parents representative of slash pine as it existed in 1955. The improved loblolly taxon consisted of open-pollinated seed from 17 superior parents, mostly from the Atlantic Coastal Plain (details in Chapter 3). The hybrids were produced using pollen mixes from loblolly pine or the Caribbean pines (slash was used always as the female, details in Chapter 4). Pollen for all three sources of Caribbean pine was obtained from the Queensland Forest Service in Australia. The pollen from improved loblolly pine to produce the PEE x PTA hybrid was obtained mainly from the Atlantic Coastal Plain from Georgia and Florida.

Sixteen families in each taxon were planted per location, but 18 PEE, 17 PEU, 17 PTA, 19 PEE x PTA, 20 PEE x F1H, 18 PEE x PCH and 17 PEE x PCB families were planted across the 11 site tests (without counting some bulked lots for PEE x PCH and PEE x PCB). Seven PEE mother trees were consistent across all hybrid crosses and within the PEE taxon across all sites and hybrid taxa

Some of the 30 hybrid crosses did not yield sufficient seed or seedlings for planting as a single family in all sites as initially designed. Thus, for the hybrids PEE x PCH and PEE x PCB only three sites have 16 "single" families. For five more sites, six bulks of PEE x PCH families were formed using two or three families of this hybrid cross but planted in eight sites. For the same reason, five bulks of two to four PEE x PCB families were created and planted in eight sites. The coldest sites, KC, IP and DOF (see Table 2-1), were not planted with the PEE x PCH hybrid.

Seed collection, seedling production and field implementation are fully described in Chapters 2 and 4. At each site, two cultural management intensities were established, intensive, labeled as High, and less intensive, labeled as Low (described in Chapter 2). All tip moth incidence analyses were performed in the less intensive treatment, since the intensive treatment received insecticide applications.

As part of the pre-planting site preparation, weed control, chopping, raking, burning, and bedding were done as needed (Table 2-2). For the low treatment, no fertilization was used except for the SJL location where phosphorus was added at establishment. No weed control was used during the first three growing seasons, except for mowing prior to the winter measurement to facilitate data recording. Also, in the low treatment no insecticide was applied for the control of tip moth in all sites, except for two locations. PCA and GIL sites received one insecticide application during the second and third growing seasons (1996 and 1997). Due to their low tip moth incidence, the PCA and GIL sites were not used in most analyses.

Variables Measured

The following variables were measured:

1. Height was assessed at one, two and three years of age in the winters of 1995-96, 1996-97 and 1997-98, and was measured as height to the highest terminal bud.

2. Terminal tip moth attack was assessed in the 1995-96 winter (1 year after planting) and was scored as number of attacks in that year to each tree's terminal shoot. Second and third measurement was not accomplished because trees were so tall than accurate measurements were though not being adequate.

3. Lateral tip moth attack was assessed at one, two and three years of age. It was recorded as percentage of lateral branches with evidence of tip moth attacks. This percentage was created by the independent observations of two observers for each tree. For the first year, all lateral branches were observed on each tree (each observer scored half the tree). Measurements of attacked tips at 2 and 3 years of age were taken from a sample of 10 branches by each observer. In all cases, the score for each tree was converted to the percentage of lateral buds showing evidence of attacks. Terminal or lateral tips were counted as attacked if they exhibited browning, curling tips, die back, or resin globules. Terminal attack was not counted as lateral attack.

Tip Moth Identification

To identify which species of tip moth were attacking PEE, PTA, and their F1 hybrid PEE x PTA, insect samples were collected from four sites with high infestation rates. Species of *Rhyacionia* are distinguishable by several characteristics in its adult, larvae and pupae stages (Miller 1960; Yates 1960, 1967a). Since large quantities of pine tip moths are in the readily identifiable pupae stage during the winter (Miller and Wilson 1964), all samples were collected at the end of second growing season from the low treatment. Pupae collection on the high treatment was not accomplished because the insecticide application reduced tip moth incidence. Five families per taxon were sampled in each site. The goal was to sample 7 pupae per family-block, but due to the lack of successful attacks in some sites, some samples were smaller than initially planned. A successful attack is defined as when a pupa is found living inside a pine tip, and will likely mature into an adult moth. It was noted that less than 2 damaged branch tips were needed to get one pupa in PTA or PEE x PTA, while 4 to 5 damaged terminal were needed to get one pupa in PEE. Therefore, 15 or more apparently infested tips were collected for each family in each block. For PEE, the pupa collection was smaller since many larvae had died before the pupa stage.

After collection, pine tips were dissected to detect the presence of pupae. Species identification was according to the procedures of Yates (1967a) in which the size of the pupae, the shape of the frontal horn and the texture of the surface area between the eyes were used as key features for identification.

Statistical Analysis

Management effects on tip moth incidence

A series of single-site analyses of variance were performed to compare the efficiency of insecticide application to reduce tip moth attacks, i.e. treatment differences. These ANOVAs were performed in sites where tip moth incidences were high in the low treatment in which no insecticide was applied, and where cooperators made several insecticide application in the high treatment (from 2 to 7 applications across sites and years). Four sites satisfied these criteria and were used for first-year lateral data and one site was suited for second-year lateral attack data. Phenotypic variances among all six blocks nested in treatments were similar in each of these sites. Consequently, individual raw data were used for analyses, with a default probability value of 0.05 to show significance. Treatment, taxon and treatment by taxon interaction were fixed effects and tested with a model based on model (2-1) after including the random effect of the family by block interaction term (bf_{ijkm}):

$$Y_{ijkmn} = \mu + \alpha_i + b_{j(i)} + \tau_k + \alpha\tau_{ik} + b\tau_{ijk} + f_{m(k)} + \alpha f_{im(k)} + bf_{ijm(k)} + e_{ijkmn} \qquad (5\text{-}1)$$

where: Y_{ijkmn} = is the nth observation of the mth family of the kth taxon in the jth block at the ith treatment, and all other terms are described in Model (2-1).

Taxon comparisons and hybrid vigor

A series of analyses of variance (ANOVAs) using only data from the low cultural treatment were performed to compare taxon differences for terminal attacks and lateral attacks. To accomplish this objective, data across sites (pooled analyses) and single-site analyses were performed. For all ANOVAs individual tree and untransformed data were used. Since less than 1.4% of the trees had more than 3 attacks on the same terminal, these values were converted to 2. For the trimodal analysis, data for terminal attacks in the first year, 0, 1 and 2 terminal attacks represented 54%, 31% and 15% of the observations, respectively.

To test the main effects of site, taxon and site by taxon interactions, pooled analyses were performed for sites where the most susceptible taxon had more than 20% of the laterals attacked. Data from seven sites were pooled for analyses for terminal and lateral attacks during the first year, and four sites for second-year lateral attacks. No ANOVA is reported for the third year since no taxon had more than 20% attacks during that time. Also, 10 sites were measured during the first year, while all 11 sites were measured for years 2 and 3. The model used for the pooled analyses was:

$$Y_{tjkmn} = \mu + s_t + b_{j(t)} + \tau_k + s\tau_{tk} + b\tau_{tjk} + f_{m(k)} + sf_{tm(k)} + bf_{tjm(k)} + e_{tjkmn} \qquad (5\text{-}2)$$

where: Y_{tjkmn} is the n^th^ observation of the m^th^ family of the k^th^ taxon in the j^th^ block at the t^th^ site,

μ is the population mean,

s_t is the random variable for site ~*NID* $(0, \sigma^2_s)$,

$b_{j(t)}$ is the random variable for block within site ~ *NID* $(0, \sigma^2_b)$,

τ_k is the fixed effect for taxon (PEE, PTA, PEE x PTA, PEE x F1H, PEE x PCH, PEE x PCB, or PEU),

$s\tau_{tk}$ is the random interaction site by taxon ~*NID* $(0, \sigma^2_{s\tau})$,

$b\tau_{tjk}$ is the random interaction block (site) by taxon ~ *NID* $(0, \sigma^2_{b\tau})$,

$f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$,

$sf_{tm(k)}$ is the random interaction site by family ~*NID* $(0, \sigma^2_{sf})$,

$bf_{tjm(k)}$ is the random interaction block (site) by family (taxon) ~*NID* $(0, \sigma^2_{bf})$,

e_{tjkmn} is the error term ~*NID* $(0, \sigma^2_e)$;

where t=1,...7 or 4 sites; j= 1,2,3 blocks; k= 1,...7 taxa; m=1,...16 families per taxon; and n=1, ...5 trees.

The model for the single-site analyses was derived from the complete model (5-2), where the number of sites (s_i) equals one. The model used is obtained by dropping all terms from (5-2) relating to site (i.e., dropping all terms with subscript *t*):

$$Y_{jkmn} = \mu + b_j + \tau_k + b\tau_{jk} + f_{m(k)} + bf_{jm(k)} + e_{jkmn} \qquad (5\text{-}3)$$

where: Y_{jkmn} is the nth observation of the mth family of the kth taxon in the the jth block. All other terms were described in model (5-2)

For all single-site and pooled analyses, PROC GLM (SAS Institute 1988) was used to test the significance of random effects. Significance levels and estimated means (using LSMEANS option) for the fixed effect taxon were obtained from PROC MIXED with the Satterthwaite option (Littell *et al*. 1996). A default probability value of 0.05 was established to show significance, unless otherwise specified.

To compare taxa differences on the basis of tip moth attacks, single degree-of-freedom contrasts were computed for both single site and pooled analyses. For example, specific null hypotheses for contrasts were: 1) There are no differences between improved slash and improved loblolly (PEE *vs*. PTA); 2) There are no differences between improved and unimproved slash (PEE *vs*. PEU); 3) There are no differences between PEE x PTA and the average performance of PEE and PTA; and 4) There are no differences between PEE x F1H and the average performance of PEE and PEE x PCH. The last two contrasts were done to determine whether or not hybrid vigor was expressed in the hybrid taxa for all traits measured. These contrasts were calculated based on model (4-3).

Family level analyses

The goal was to determine the level of genetic control for tip moth resistance in all taxa. These analyses were conducted separately from each taxon using only data from the low treatment. Thus, estimates of variance components for family, site by family, site by block and error were calculated for each taxon with a pooled analysis across sites. The model was derived from the complete model (5-2), where the number of taxa (τ_k) equals one. The model used was obtained by dropping all terms from (5-2) relating to taxon (i.e., dropping all terms with subscript *k*):

$$Y_{tjmn} = \mu + s_t + b_{j(t)} + f_m + sf_{tm} + bf_{tjm} + e_{tjmn} \qquad (5\text{-}4)$$

where: Y_{tjmn} is the nth observation of the mth family in the the jth block at the tth site. All other terms were described in model (5-2), but site and block effects were considered as fixed effects.

Variance components were estimated by PROC MIXED, with the restricted maximum likelihood method, REML (Littell *et al.* 1996). For pooled analyses, lateral attack was standardized by dividing each observation in a site-treatment-block combination by the corresponding square root of the phenotypic variance for that block to remove the effects of scale (Visscher *et al.* 1991; Hodge *et al.* 1996).

Single-site analyses were also performed to get estimates of variance components for each taxon-site combination. The model used was derived from the model (5-4), where the number of sites (s_t) equals one. The model used was obtained by dropping all terms from (5-4) relating to site (i.e., dropping all terms with subscript *t*):

$$Y_{jmn} = \mu + b_j + f_m + bf_{jm} + e_{jmn} \qquad (5\text{-}5)$$

where: Y_{jmn} is the nth observation of the mth family in the jth block. All terms are described in model (5-2), but block effect was considered as a fixed effect.

Heritabilities

The goal was to estimate pooled heritabilities (h^2) and single-site heritabilities (h^2_b) for first-year terminal, and first- and second-year lateral attacks, for each taxon, as a measure of the genetic control for tip moth resistance. Estimates of variance components were used from pooled analyses with model (5-4) to estimate h^2 and from single-site analyses with model (5-5) to estimate h^2_b.

The open-pollinated families in the PEE, PEU and PTA taxa were assumed to be half-sib families; hence, the variance component for families (σ^2_f) can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A) (Falconer and Mackay 1996). For the hybrids, a hybrid heritability (h^2_h), was calculated as the proportion of 4 times the hybrid family variance (σ^2_{fh}) over the total phenotypic variance.

These h^2_h values for hybrids may be bigger than those of pure species because, in the hybrids, additive and non-additive variance are confounded in σ^2_{fh} and gene frequencies in parental species may be different (Wei *et al.* 1991). Therefore, estimates of heritability (h^2 or h^2_h) for each taxon were calculated as:

$$h^2 \text{ or } h^2_h = 4^* \sigma^2_f \;/\; \sigma^2_f + \sigma^2_{sf} + \sigma^2_p + \sigma^2_w \qquad (5\text{-}6)$$

where values were obtained from model 5-4, and $\sigma^2_p = \sigma^2_{bf}$ and $\sigma^2_w = \sigma^2_e$.

Lastly, biased heritabilities (h^2_b or h^2_{bh}) were estimated for each taxon-site combination with the following model:

$$h^2_b \text{ or } h^2_{bh} = 4 * \sigma^2_f \; / \; \sigma^2_f + \; \sigma^2_p \; + \; \sigma^2_w \tag{5-7}$$

where values were obtained from model 5-5, and $\sigma^2_p = \sigma^2_{bf}$ and $\sigma^2_w = \sigma^2_e$.

Results and Discussion

Efficiency of Control of Tip Moth Attack

Single-site analyses indicated that insecticide application successfully reduced tip moth attacks in those areas highly affected by tip moth (Figure 5-1). Lateral and terminal attacks were lower in the high treatment for all five sites analyzed (at least $p<0.02$). These results suggest that the pesticides must have been effective in controlling tip moth because without pesticides more attacks are expected in intensively-managed areas. However, the effectiveness of insecticide application may be confounded with the effect of fertilizer and weed control in accelerating stand development, so taller trees can escape the attack for being outside the susceptible size class. In any case, significant increases in tip moth attacks have been recorded in sites which received intensive management and weed control without pesticides (Berisford and Kulman 1967; Hood *et al.* 1988). This may be due to an increased tree visibility, a decreased habitat for parasites or tip moth's predators or the increased pine biomass providing more feeding sites (Nelson and Cade 1984). Thus, insecticide application, after the species selection, has been the preferred practice to control tip moth (Stephen *et al.* 1982) especially when using a spray-timing model for pesticide applications to target the most vulnerable life stages of pine tip moth (Berisford *et al.* 1984, *et al.* 1989; Gargiullo *et al*. 1985).

In some of these highly affected areas, treatment by taxon interactions were significant ($p<0.05$), but overall, no taxon rank changes where detected across treatments. Improved loblolly pine (PTA) and the PEE x PTA hybrid were the most attacked taxa with (high treatment) or without (low treatment) insecticide application

Taxon Comparisons for Tip Moth Incidence

Incidence of tip moth attacks decreased with age for both treatments (see Figure 5-2 for low treatment). Mean lateral attacks in the low treatment was highest during the first growing season. For the seven most tip-moth affected sites, 50%, 14% and 4% of lateral tips were attacked after the first, second and third growing season, respectively (Figure 5-2).

Highly significant differences for first-year attacks were found among sites. The reasons for different stands having radically different tip moth populations and/or damage are not fully understood (Berisford 1988), but they are related to tree species, weather, site quality, cultural practices, and natural enemies.

The pooled analysis using only sites with moderate to heavy incidence levels showed significant differences for taxon and site by taxon interaction for all traits (Table 5-1). However, for first-year terminal, and for first- and second-year lateral attacks, no important rank changes were detected across sites. PTA and PEE x PTA were consistently the taxa most attacked by tip moth across all sites; there were smaller differences among the other five taxa (Figures 5-3 and 5-4).

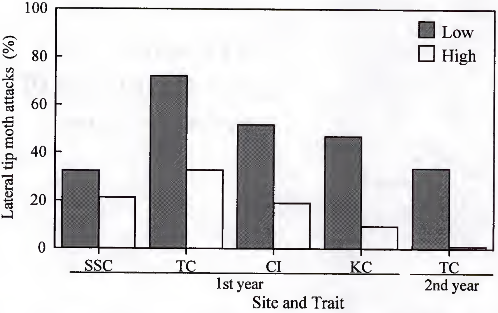


Figure 5-1. Percentage of lateral tips attacked by tip moth in the high and low cultural treatments. Averages are combined across all seven taxa in each site where the low treatment had high incidence of tip moth damage and several insecticide applications were done in the high treatment. Single-site ANOVA's showed that treatments differed significantly at all sites (at least $p<0.05$). Treatment-by-taxon interactions were significant twice but no taxon rank changes in incidence were noted between treatments.

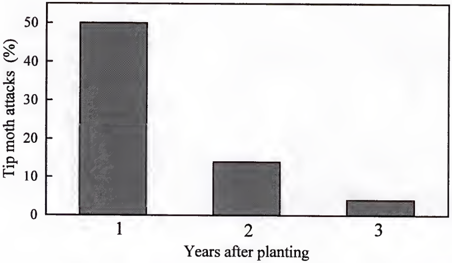


Figure 5-2. Average lateral tip moth attacks in percentage in the low treatment across years. Mean values are averaged of all seven taxa for the seven sites highly infected with tip moth.

Table 5-1. Analysis of first- and second-year data pooled across sites in the low treatment for lateral and terminal tip moth attacks[a].

Source	First year					Second year		
	Terminal			Lateral		Lateral		
	DF	F value	Pr > F	F value	Pr > F	DF	F value	Pr > F
SITE	6	11.79	0.0001	12.65	0.0001	3	1.45	N.S.
TAXON	6	35.61	0.0001	20.49	0.0001	6	4.46	0.0075
[b]Hybrid Vigor in PEE x PTA	1	8.84	0.0049	9.17	0.0036	1	4.84	0.0425
[c]Hybrid Vigor in PEE x F1H	1	1.95	N.S.	0.04	N.S.	1	0.07	N.S.
PEE *vs.* PTA	1	101.8	0.0001	40.66	0.0001	1	12.53	0.0027
PEE *vs.* PEE x PCH	1	7.12	0.0120	1.01	N.S.	1	2.02	N.S.
PEE *vs.* PEE x PCB	1	1.03	N.S.	3.90	0.0528	1	0.08	N.S.
PEE x PCH *vs.* PEE x PCB	1	12.91	0.0009	7.49	0.0081	1	0.40	N.S.
SITE*TAXON	35	1.73	0.0224	6.12	0.0001	16	6.50	0.0001
FAMILY (TAXON)	130	1.66	0.0001	1.39	0.0057	129	1.52	0.0024
SITE*FAMILY (TAXON)	588	0.99	N.S.	1.27	0.0002	261	0.93	N.S.
ERROR	8749					4580		

a. ANOVA of first-year data was for the seven sites with moderate to high tip moth incidence. In the second year, lateral attacks were analyzed pooling four sites. Lateral attacks ranged across all taxa from 10% to 72% in the first year and from 8% to 21% in the second year. The most attacked taxon had in each site from 21% to 93% of and from 21% to 90% of lateral attacks, first year and second year, respectively.

b. Hybrid vigor of the PEE x PTA hybrid was analyzed by: PEE x PTA / (0.5 PEE + 0.5 PTA).

c. Hybrid vigor of the PEE x F1H backcross hybrid was analyzed by:
PEE x F1H / (0.5 PEE + 0.5 PEE x PCH).

Even though the PEE x PTA hybrid had less terminal attacks than PTA (p =0.02, Figure 5-3), negative hybrid vigor was detected since the mean value was closer to the susceptible taxon, PTA. Further, the hypothesis PEE x PTA was intermediate to parental taxa was rejected (p<0.005, Table 5-1). First- and second-year evaluations indicated a negative hybrid vigor for lateral attack in PEE x PTA, with values across sites being similar to PTA (Table 5-1, Figure 5-4). Therefore, crossing loblolly by slash pine did not reduce tip moth attacks in loblolly pine. Grigsby (1959) using few crosses, found that hybrids between loblolly and slash pines were more resistant to tip moth than was loblolly pine. This was not the case here for lateral attacks.

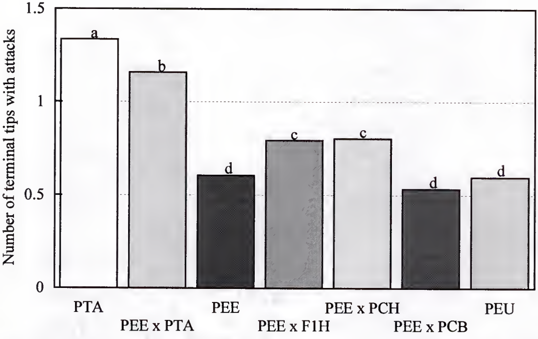
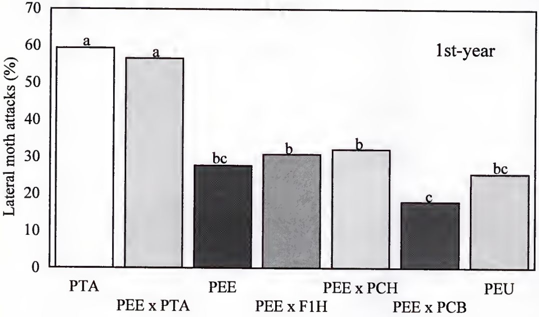


Figure 5-3. Average number of terminal tips attacked by tip moth after the first-year growing season for improved slash pine (PEE), unimproved slash pine (PEU), loblolly pine (PTA) and the hybrids slash x loblolly pine (PEE x PTA), slash x *caribaea* var. *bahamensis* (PEE x PCB), slash x *caribaea* var. *hondurensis* (PEE x PCH) and the backcross slash x PEE x PCH (PEE x F1H). Site by taxon interaction was significant, but no meaningful taxon rank changes were detected, so averages are combined across seven moderate to highly tip-moth attacked sites. Taxon was highly significant and some specific contrast are presented in Table 5-1. Taxon means with same letter are not significantly different at p = 0.05.



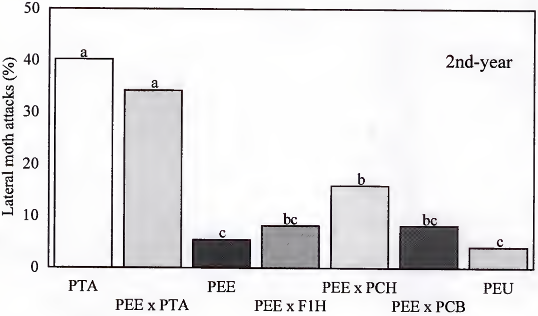


Figure 5-4. Average lateral tip moth attacks in percentage in the low treatment for first-year and second-year after planting. Taxa included are improved slash pine (PEE), unimproved slash pine (PEU), loblolly pine (PTA) and the hybrids slash x loblolly pine (PEE x PTA), slash x *caribaea* var. *bahamensis* (PEE x PCB), slash x *caribaea* var. *hondurensis* (PEE x PCH) and the backcross slash x PEE x PCH (PEE x F1H). First-year results included seven sites highly infected with tip moth and second-year results included four sites highly infected with tip moth. Taxon was highly significant and specific contrasts are presented in Table 5-1. Taxon means with same letter are not significantly different at $p = 0.05$.

No significant differences were detected between improved and unimproved slash pine, i.e., PEU was as tip moth resistant as PEE. In general, the PEE x PCB hybrid was somewhat less attacked by tip moth than PEE x PCH hybrid or the PEE x F1H backcross hybrid. For lateral tip moth attacks, PEE x PCB hybrid was the least attacked of all taxa during the first year (Figure 5-4).

Tip Moth Identification

Slash pine was significantly less attacked by tip moth than loblolly pine, supporting conclusions from other studies (e.g., Yates 1960; Hertel and Benjamin 1977; Berisford 1988). Five hundred sixty-five pupae were obtained at the end of the second-year from two locations in north Florida and two locations in south Georgia. Ninety-six percent of the pupae collected were Nantucket tip moth, 2% were Subtropica tip moth and 2% were Pitch-pine moth pupae (*R. rigidana* Fernald). There were no differences among taxa in the types of moths identified since the frequency of tip moth species were similar across taxa (Table 5-2). Subtropical and Pitch-pine moths are scarce in Georgia and north Florida (Miller 1960; Berisford *et al.* 1992). Other studies have indicated that the Nantucket tip moth prefers loblolly pine, while the Subtropica prefers slash pine (Merkel 1963; Yates 1966; McGraw 1975; Hertel and Benjamin 1977; Hood *et al.* 1988). For example, Hertel and Benjamin (1977) studying three locations in north-central Florida found that all tip moth attacks on loblolly pine were done by Nantucket tip moth, whereas more than 95% of such attacks on slash pine were done by Subtropica tip moth. This was not the case here.

Table 5-2. Number and percentage (in parentheses) of pupae collected on each taxon. Moth identification was made on samples on the second year over four sites according to the procedures of Yates (1967a).

PINE TAXA	TIP MOTH TAXA			Total
	Nantucket	Subtropica	Pitch-pine	
PTA	265 (95 %)	5 (2 %)	8 (3 %)	278 (49 %)
PEE x PTA	207 (96 %)	4 (2 %)	5 (2 %)	216 (38 %)
PEE	70 (98 %)	1 (2 %)	0 (0 %)	71 (13 %)
Total	542 (96 %)	10 (2 %)	13 (2 %)	565 (100 %)

Family Level

In general no significant differences among families in tip moth attacks were found in any single-site analysis performed for any taxon (model 5-5). Pooled analyses (model 5-4) for PTA, PEU and the PEE x PCB hybrid indicated no significant differences among families in any year for terminal or lateral attacks. For PEE and the PEE x PCH hybrid, family differences were found for first-year terminal attack and second-year lateral attack. The other two hybrids, the PEE x PTA and the PEE x F1H backcross hybrid, showed family differences for one of the three traits (first-year terminal attack for PEE x F1H and second-year lateral attack for PEE x PTA).

As a result of small differences among families, the estimates of heritability were quite low for all measures of tip moth incidence (Tables 5-3 and 5-4). The estimates of unbiased heritabilty (h^2 or h^2_h) for loblolly pine indicated little if any genetic resistance to tip moth, at least for the traits measured. The hybrid PEE x PTA showed a little more family variation for tip moth resistance, since hybrid heritabilities were higher than heritability in PTA. However, additive and non-additive variance may be confounded, inflating the size of

Table 5-3. Mean and range (in parentheses) of single-site heritability estimates (h^2_b) and pooled-site heritabilities (h^2) for terminal tip moth attack for the pure taxa and the hybrids (hybrid heritability, h^2_h). All analyses were performed in the low treatment with seven sites. These seven sites ranged across all taxa from 10% to 72% of lateral attacks, where the most attacked taxon had in each site from 21% to 93% of lateral attacks.

TAXON	h^2_b or h^2_{hb}	h^2 or h^2_h
PTA	0.05 (0.0 - 0.21)	0.01
PEE x PTA	0.06 (0.0 - 0.30)	0.02
PEE	0.04 (0.0 - 0.10)	0.03
PEE x F1H	0.14 (0.0 - 0.27)	0.05
PEE x PCH[a]	0.15 (0.0 - 0.55)	0.17
PEE x PCB	0.08 (0.0 - 0.31)	0.02
PEU	0.10 (0.0 - 0.40)	0.01

a. Analyses with 6 sites.

Table 5-4. Mean and range (in parentheses) of single-site heritability estimates (h^2_b) and pooled-site heritabilities (h^2) for lateral tip moth attacks for the pure taxa and the hybrids (hybrid heritabilty, h^2_h). All analyses were performed with standardized data for moderate to heavily attacked sites. Seven and four sites were used for first and for second-year lateral attacks, respectively. Lateral attacks ranged across all taxa from 10% to 72% for first-year, and from 8% to 21% for second-year analyses. The most attacked taxon had in each site from 21% to 93% attacks in the first year and from 21% to 90% attacks in the second year.

TAXON	First-year lateral attack		Second-year lateral attack	
	h^2_b or h^2_{hb}	h^2 or h^2_h	h^2_b or h^2_{hb}	h^2 or h^2_h
PTA	0.14 (0.0 - 0.44)	0.01	0.07 (0.0 - 0.18)	0.00
PEE x PTA	0.10 (0.0 - 0.49)	0.02	0.07 (0.0 - 0.27)	0.07
PEE	0.12 (0.0 - 0.28)	0.04	0.11 (0.0 -0.42)	0.20
PEE x F1H	0.15 (0.0 - 0.49)	0.04	0.09 (0.0 - 0.24)	0.05
PEE x PCH[a]	0.13 (0.0 - 0.60)	0.02	0.22 (0.0 - 0.44)	0.03
PEE x PCB	0.05 (0.0 - 0.20)	0.02	0.12 (0.0 - 0.32)	0.00
PEU	0.09 (0.0 - 0.40)	0.04	0.01 (0.0 - 0.03)	0.01

a. Analyses with 6 and 2 sites for first and second-years, respectively.

hybrid heritabilities (Wei *et al.* 1991).

Slash pine showed some degree of genetic control for second-year lateral attack (h^2 =0.20), as did the PEE x PCH hybrid for terminal attack (h^2_h =0.17). A few sites estimates of single-site heritabilities (h^2_b or h^2_{hb}) indicated a moderate genetic control; however, there was no a clear relationship between the amount of tip moth attacks and the heritability estimates from each site.

General Discussion and Conclusions

Tip moth attacks were the highest in the first year, then declined in the subsequent years to an insignificant level after the third growing period. This behavior was detected in both high and low treatments. In high treatment, tip moth incidence was drastically reduced. More insecticide application were used during the second year, but also the effect of treatments in accelerate stand development may change the rate of reduction of tip moth attacks across years. Yates (1966) and Hood *et al.* (1985) found that slash pine was most susceptible to tip moth during the first year. Others have found under operational culture that tip moth attacks were relatively high in the second year, and either stabilized or declined in the third and following years (Cross *et al.* 1981; Thomas *et al.* 1982).

The Nantucket tip moth was the primary tip moth species found in the four sites sampled. Nantucket tip moth causes more damage than Subtropical because it develops more generations in a single season. For example, in northern Florida, Nantucket tip moth has five or six generations, double the number of generations of Subtropica or Pitch-pine moth (Miller 1960; McGraw 1975; Hedden *et al.* 1980). Further, successful control of *Rhyacionia* spp. with contact insecticides depends on the amount and accurate timing of the insecticide applications (Yates 1967b; Berisford 1982), which varies according to tip moth generation (Gargiullo *et al.* 1983; Berisford *et al.* 1984).

Pure loblolly pine (PTA) and the PEE x PTA hybrid were significantly more attacked by tip moth than slash pine or any slash x Caribbean hybrid. Although no accurate counts were made, for slash pine four to five tips were required to get one pupa (a successful attack). Meanwhile, less than two pine tips were needed to get one pupa for loblolly pine and the PEE x PTA hybrid. It seems likely then that most of the adult tip moths developing on the site were from loblolly pine and the PEE x PTA hybrid, because of higher incidence of tip moth on loblolly pine and the fact that for each attack more living pupae were found in loblolly pine and the PEE x PTA hybrid. Yates (1962;1966) found that if tip moth eggs are laid with equal frequency on slash and loblolly pine shoots, greater larval mortality occurs on slash pine.

The frequency of tip moth attacks in slash pine might have been lower if the species had been grown in a single species plantation. Due to the experimental design, the insects could have spread into the surrounding resistant slash pine trees due to their proximity to a susceptible PEE x PTA hybrids and loblolly pines.When insect population density is very high (outbreaks), the insect can spread into the surrounding healthy trees (Scriven and Luck 1980; Berryman 1987; Speight and Wainhouse 1989).

Family differences for tip moth attacks were all but absent in loblolly pine. Heritability estimates for tip moth resistance were very low, indicating almost no genetic control to resist tip moth attacks. In other words, all 17 loblolly pine families seemed to be equally susceptible to tip moth attack. The lack of evidence of genetic control may be due to the low number of families sampled or due the way that the traits were measured. Moreover, the proximity to heavily infested trees and synchrony between the emergence of adult moths and the availability of susceptible pine tips accentuate the apparent susceptibility of an individual (Scriven and Luck 1980). Thus, resistant families or individual trees may appear less resistant if grown in the proximity of susceptible trees. A little more genetic variation was detected among the PEE x PTA families tested, but this hybrid cross does not seem useful for increasing tip moth resistance as an F1 hybrid since incidence of tip moth attacks were quite similar to those on pure loblolly pine.

Cade and Hedden (1989) analyzing 12 open-pollinated families in six locations in North Carolina found family differences in loblolly pine for tip moth infestation levels and for percent of growth loss. Also, Hertel and Benjamin (1975) studying 14 sources in one location indicated that although loblolly pine is very susceptible to tip moth attacks, there is some evidence that resistance may vary by seed source. In one test in Georgia, Schmitling and Nelson (1996) found, variability among provenances of loblolly pine with respect to tip moth susceptibility Atlantic Lower Coast and Florida provenances were susceptible and Livingston Parish provenance was more resistant to tip moth attacks.

Slash pine and the slash x Caribbean hybrid families experienced less tip moth attacks than the PTA and PEE x PTA. Also, there was some evidence of a small amount of genetic control to avoid attacks by tip moth among the families in these taxa. In this study, a pine tip with tip moth attack was considered as any tip with resin globules, browning or dead tips. Most of the counts of attacks in the slash pine and the slash x Caribbean hybrids were just resin globules. Tips damaged by tip moth in the loblolly pine and the PEE x PTA hybrid families were primarily browning or dead tips. The evidence here and in the literature suggested that resistance to tip moths in slash pine seems both quantitative and qualitative in nature, and this study only measured the quantitative resistance.

Even with a high tip moth incidence, loblolly pine was taller than slash pine at three years of age (data from Chapter 2). Price (1991) found ample evidence that many shoot-borer insects prefer plants that have grown vigorously, because larvae survive better in larger buds on long shoots. However, fast-growing species can compensate for damage with vigorous growth. Apparently extremely rapid growth of host trees to some extent enables them to recover from successful attacks and to escape the susceptible stage sooner (Ross and Berisford 1990; Sun 1990).

Slash pine and the slash x Caribbean hybrids appear more tip moth resistant, because they can avoid or reduce the probability of being a host (antixenosis or non-preference, Painter 1951; Kogan and Ortman 1978) and kill larvae (antibiosis). Antibiosis may explain why many buds on slash pine were found with an abandoned mine full of resin without a living larva. On the other hand, loblolly pine may present tolerance to tip moth damage, as Wakeley and Coyne (1973) and Sun (1990) have found that loblolly pine has the ability to recover from the tip moth damage. Thus, selecting trees with asynchronous growth flushes (Scriven and Luck 1980), inter-provenance crosses (Hertel and Benjamin 1975; Schmitling and Nelson 1996) and quick recovery after tip moth attacks (Stephen *et al.* 1982; Andersen *et al.* 1984) have been mentioned as possible strategies to reduce impacts of tip moth in loblolly pine. Unlike antixenosis and antibiosis, tolerance is not part of an insect-plant interaction and involves only plant characteristics (Speight and Wainhouse 1989). Tolerance to tip moth damage is potentially very stable, because it produces a weak selection pressure on the insect population (Speight and Wainhouse 1989).

CONCLUSIONS

A large field study was installed in 1995 by cooperators of the Cooperative Forest Genetics Research Program (CFGRP) over 11 field sites to determine the yield potential of four slash pine hybrids compared to improved loblolly pine, and improved and unimproved slash pine. The seven taxa compared in this study were: 1) slash pine x *P. caribaea* var. *hondurensis* (PEE x PCH); 2) the backcross of slash pine x the F1 hybrid between slash x *P. caribaea* var. *hondurensis* (PEE x F1H); 3) slash pine x *P. caribaea* var. *bahamensis* (PEE x PCB); 4) slash pine x loblolly pine (PEE x PTA); 5) improved loblolly pine (PTA), 6) improved slash pine (PEE); and 7) unimproved slash pine (PEU). The goal was also to compare the responses of all taxa to both low and high silvicultural management intensities. The high treatment included fertilizer, weed control and insecticide application after planting. The purpose of this dissertation project was to evaluate this large experiment at three years of age to quantify results for traits related to early performance and adaptability such as height growth, rust incidence, tip-moth incidence and cold damage.

This dissertation was divided in four major sections. In Chapter 2, the focus was on the taxa comparisons, improved loblolly *vs.* improved slash pine, and improved slash pine *vs.* unimproved slash pine. Results from assessment at three years of age indicate that improved loblolly pine was consistently taller with less rust incidence than slash pine in both high and low intensive cultures, with bigger differences in the high treatment. The early superiority of loblolly pine was only partially due to its lower rust incidence. Since loblolly pine is a faster growth species at this early age, evaluation at later ages are needed to really assess the superiority of loblolly pine over slash pine.

A 5% increase of rust incidence was produced by increasing intensive management (29.2 to 33.6 % across PTA, PEE and PEU). However, the increase in cultural management did not alter the ratios of infection percentages of PTA and PEE over PEU infection, and these ratios were essentially constant across all sites. Significant genetic gain from breeding for rust resistance was detected at this age for slash pine. When 50% of PEU trees were infected, 36.8% of PEE trees were infected, which met the expectation based on the breeding values calculated in the CFGRP. For height growth, PEE was 4% and 8% taller than PEU in less intensive and intensive treatment, respectively. Evaluation at later ages are necessary to assess the genetic gains for volume on slash pine, to determine if realized gains meet the prediction based on the breeding values. For all taxa, the effect of culture on accelerating the stand development should be studied in future evaluations.

The impact of intensive treatment on heritability and genotype x environment interaction (gxe) was investigated in Chapter 3 by analyzing the performance of the families comprising the three native taxa of PTA, PEE and PEU. Results for third-year fusiform rust infection indicated that single-site heritabilities for rust in the binary scale ($h^2_{B\,0,1}$ =0.18) and in the underlying scale ($h^2_{B\,und}$=0.29) were not affected by site nor by the increase in culture management intensity. These estimates indicate that rust resistance is one of the more heritable traits of commercial importance other than wood properties.

Further, highly consistent family rankings across sites ($r_{B\text{-site}}$=0.90) and across management intensities ($r_{B\text{-treat}}$=0.97) were found for rust incidence. These results are based on a relatively acceptable number of families (52 families) and they suggest that there is no need to match specific families to either sites or management regimes. However, the results of Schmidt *et al.* (1999) indicated that slash pine families are not always stable in rust resistance across sites and planting years. Thus, decisions on single-family deployment in commercial plantations should consider potential instability for rust resistance, and more research may be needed on this disease over intensive silviculture across sites and planting years. The moderate h^2 and stability of family performance explain part of the success in increasing resistance to this disease.

For third-year height growth, family rankings were less influenced by environmental differences among treatments on the same site ($r_{B\text{-treat}}$=0.87) than by differences among sites ($r_{B\text{-site}}$=0.57). These early results imply that stable rankings for height may be expected as cultural management increases. However, a few families were more responsive to culture than others. If this trend continues at later ages, families with vigorous growth maybe useful for family deployment under high intensive culture. Another advantage of high culture was the smaller site by family interaction (higher $r_{B\text{-site}}$ value) than low culture, meaning family ranking for height were more stable across sites in the intensive culture treatments.

Moreover, in the intensive treatment, additive variance was reduced by 6% and environmental error decreased by 25%. This resulted in higher heritability for the high treatment as compared to low treatment (h^2_B = 0.3 *vs.* 0.2, averaged over all three taxa and all sites). The higher heritability for height growth in the high culture implies that genetic gains from progeny testing are higher in intensive culture. Further, the higher heritability in the high culture along with little GxE between treatments ($r_{B\text{-}treat}=0.87$) implies that progeny testing with intensive culture could have advantages for operational deployment in either culture. These results for h^2 at three years of age need to be assessed at later age for comparison. In particular, continuous applications of fertilizer may be needed to maintain this higher h^2 in the high treatment. Also research on the effects of fertilizer and weed control are necessary to separate which of the factors are increasing h^2.

In Chapter 4, the slash x Caribbean hybrids and PEE x PTA hybrid were compared to pure slash and loblolly pine to examine the adaptation of such hybrids to lower Coastal Plain sites (mainly in north Florida). Growth, rust incidence, and cold damage of the taxa were studied across eight sites. Results indicated that PTA was the best taxon. PEE x F1H and PEE x PCB were less affected by cold damage and taller than PEE x PCH, and had height growth similar to PEE. All Caribbean x slash hybrids were more susceptible to fusiform rust than PEE. The PEE x PTA hybrid was susceptible and closer to PEE for rust incidence. The taxon ranking for height growth was not affected by cultural treatments, but differences increased in the high treatment. Also, outstanding healthy trees were detected in all hybrid taxa.

Larger hybrid heritabilities (h^2_h) and more within-family variability for height compared to within families of parental species were detected and this may be exploited by selection within hybrid families to find outstanding recombinants. If these early results are confirmed in later years, the technique of reciprocal recurrent selection may not hold much promise since it is based on operational deployment of the F1 hybrids and none of the hybrids tested here outperformed, on average, the current pure taxa being deployed (PEE and PTA). The excellent individual trees within hybrid taxa might be useful for breeding purposes in hybrid programs that combine genes from the hybrids back with the parental PEE and PTA species in various combinations to form synthetic taxa. However, later results are needed to accurately assess the potential of these hybrids. Other traits, such as wood characteristics also need evaluation to assess overall utility of incorporating genes from these Caribbean pines.

Other hybrids with slash or possibly with loblolly pine maybe more useful. For example, crosses of slash pine with *Pinus cubensis* Griseb., a close relative of slash, show hurricane resistance and cold hardiness. This species and its hybrid with slash pine have demonstrated slow early growth that accelerates greatly by age 10-12 years (Dr. G. Nikles, pers. com.). Also, hybrids with loblolly pine with the Caribbean pines may be worth testing in the LCP. However, poor hybridization of loblolly pine with the Caribbean pines may be found, e.g., low seed production or dwarf trees as in the PEE x PTA was detected.

Finally, in the Chapter 5 the focus was on tip moth incidence in all seven taxa. Tip moth attacks were the highest in the first year, then declined in the subsequent years to an insignificant level after the third growing period. The Nantucket tip moth was the primary tip moth species found in the four sites sampled.

Pure loblolly pine (PTA) and the PEE x PTA hybrid were significantly more attacked by tip moth than slash pine or any slash x Caribbean hybrid. As matter of fact, the PEE x

PTA hybrid had more rust incidence and almost the same incidence of tip moth attacks as pure loblolly pine.

Family differences for tip moth attacks were all but absent in loblolly pine. Heritability estimates for tip moth resistance were very low, indicating almost no genetic control for tip moth resistance. The lack of evidence of genetic control may be due to the small number of families sampled or due to the way that the traits were measured. Other studies have shown some genetic control for reduction of tip moth incidence and for percent of growth loss (Cade and Hedden 1989. Schmitling and Nelson (1996) found that Livingston Parish provenance was more resistant to tip moth attacks than provenances from Florida or Atlantic Coastal, and this maybe useful in interprovenances crosses.

In any case, even with a high tip moth incidence, loblolly pine was taller than slash pine at three years of age, and this may be evidence of tolerance mechanisms to reduce impacts of tip moth. Evaluation for tip moth resistance should include evaluation for tip moth incidence and evaluation for impact of growth, which includes the ability to recover from damage.

APPENDICES

APPENDIX A

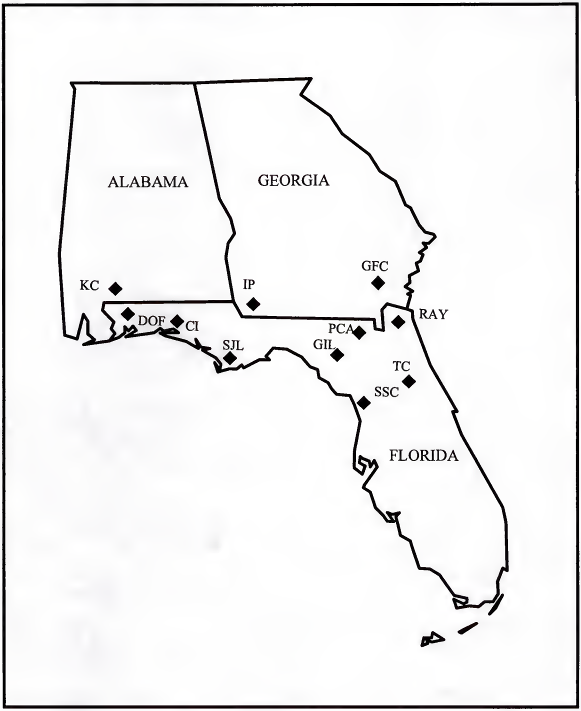
ESTIMATED BREEDING VALUES FOR RUST (R50) AND FOR VOLUME (GAINVOL) OF THE PARENTS AND OFFSPRING OF SLASH PINE

Family No. **PEE**	Breeding Values for the parents		No. Sites	Breeding Values for the offspring (30% pollen contamination)		Weighted Breeding Values for the offspring	
	R50	Gainvol		R50	Gainvol	R50	Gainvol
1	34.98	25.16	11	32.66	22.56	35.93	24.81
4	20.86	40.50	11	42.63	26.01	46.89	28.61
5	32.12	21.68	8	35.36	17.81	28.29	14.25
6	45.70	20.20	11	42.67	17.24	46.94	18.96
14	10.69	23.84	11	22.54	19.24	24.79	21.16
15	45.01	25.54	11	45.90	19.90	50.49	21.89
20	38.90	24.16	11	38.74	19.04	42.62	20.95
21	19.82	29.13	5	27.52	19.89	13.76	9.94
22	48.17	25.19	9	43.91	19.74	39.52	17.76
51	53.50	18.14	8	46.04	16.04	36.84	12.83
52	53.49	32.13	11	47.72	21.28	52.49	23.41
53	44.66	11.67	8	42.54	11.96	34.03	9.57
54	48.65	24.12	11	42.04	17.38	46.25	19.12
55	-9.18	30.12	11	16.39	20.28	18.03	22.30
56	5.32	16.47	9	25.74	14.29	23.17	12.86
57	44.57	30.68	8	41.58	22.31	33.27	17.85
58	27.09	16.36	11	34.83	12.03	38.32	13.23
59	27.08	14.40	11	37.44	11.22	41.18	12.34
Average	32.86	23.86				**37.09**	**18.29**

APPENDIX A (CONTINUED)

Family No. **PEU**	Breeding Values for the parents		No. Sites	Breeding Values for the offspring (30% pollen contamination)		Weighted Breeding Values for the offspring	
	R50	Gainvol		R50	Gainvol	R50	Gainvol
61	57.37	8.97	11	51.55	10.36	56.70	11.40
62	72.25	12.80	11	55.42	13.36	60.96	14.70
63	66.55	1.72	11	61.07	-2.43	67.18	-2.67
64	53.75	10.37	11	54.68	3.79	60.14	4.17
66	51.73	-4.07	11	44.11	-13.66	48.52	-15.03
67	63.93	7.44	11	50.21	-1.73	55.23	-1.91
68	54.72	-1.60	5	49.21	-1.47	24.61	-0.74
69	44.80	5.19	6	40.29	4.76	24.17	2.86
70	56.59	8.66	11	52.00	8.74	57.20	9.61
71	59.00	8.15	11	52.75	8.56	58.03	9.41
72	60.86	3.93	11	53.68	6.44	59.05	7.09
73	55.52	7.74	11	51.01	8.35	56.11	9.19
74	55.50	5.24	11	51.00	7.10	56.10	7.81
75	53.63	3.63	11	50.07	6.30	55.07	6.93
76	55.43	6.20	11	50.97	7.58	56.06	8.34
77	58.93	3.48	11	47.92	6.22	52.71	6.84
78	58.66	7.39	11	50.62	8.17	55.68	8.99
Average	57.60	5.60				**51.34**	**4.94**

APPENDIX B
LOCATION OF THE 11 SITES IN STUDY



APPENDIX C
SUMMARY OF THE SINGLE SITE ANALYSES FOR RUST INCIDENCE AT THREE YEARS OF AGE (SIGNIFICANCE LEVELS AND F TESTS)

SITE	TREAT	TAXON	TREAT * TAXON	CONTRASTS							
				PEE vs PEU	PEE vs PTA	PEE vs PEU			PEE vs PTA		
						High	Low	Int[1]	High	Low	Int[1]
SSC *	0.032	0.001	N.S.	0.001	N.S.	0.001	0.027	N.S.	N.S.	N.S.	N.S.
TC	0.001	0.001	0.089	0.004	0.001	0.002	0.085	N.S.	0.046	0.001	0.032
GIL	0.018	0.001	N.S.	0.001	0.003	0.004	0.003	N.S.	0.004	0.069	N.S.
RAY	N.S.	0.001	N.S.	0.047	0.001	N.S.	0.093	N.S.	0.001	0.009	N.S.
GFC	N.S.	0.005	N.S.	0.037	0.091	0.074	N.S.	N.S.	N.S.	0.096	N.S.
CI	N.S.	0.001	N.S.	0.009	0.059	0.023	0.048	N.S.	0.070	N.S.	N.S.
PCA	0.025	0.023	N.S.	N.S.	N.S.	N.S.	0.097	N.S.	N.S.	N.S.	N.S.
SJL *	N.S.	0.038	N.S.	N.S.	N.S.	0.086	N.S.	N.S.	N.S.	N.S.	N.S.
KC	N.S.	0.001	0.001	0.006	0.001	0.048	0.005	N.S.	0.002	0.001	0.005
IP	0.006	0.001	N.S.	0.055	0.024	N.S.	N.S.	N.S.	0.029	N.S.	N.S.
DOF	0.013	0.001	0.041	0.008	0.033	0.008	N.S.	N.S.	0.013	N.S.	N.S.

Note: Treat*Taxon interaction in TC and DOF were due to scale effects.

Int[1]. Interaction of that contrast with treatment. All significant interactions were due to scale effects not rank changes.

* . Rust damage <15%.

APPENDIX D

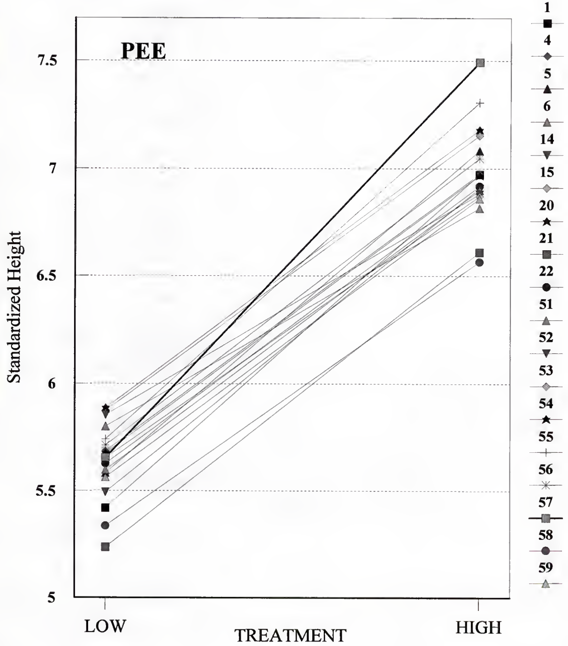
SUMMARY OF 10 SINGLE SITE ANALYSES FOR TOTAL HEIGHT AT THREE YEARS OF AGE (SIGNIFICANCE LEVELS AND F TESTS)

SITE	TREAT	TAXON	TREAT * TAXON	CONTRASTS							
				PEE vs PEU	PEE vs PTA	PEE vs PEU			PEE vs. PTA		
						High	Low	Int^1	High	Low	Int^1
SSC	0.001	0.010	0.017	N.S.	0.017	0.089	N.S.	0.081	0.009	N.S.	N.S.
TC	0.001	0.008	N.S.	N.S.	0.022	N.S.	N.S.	N.S.	0.046	N.S.	N.S.
GIL	0.035	0.001	0.088	0.010	0.001	0.025	0.085	N.S.	0.001	0.024	0.092
RAY	0.002	0.001	0.006	0.001	0.001	0.001	0.042	N.S.	0.001	0.008	0.023
GFC	0.030	0.001	N.S.	N.S.	0.001	N.S.	N.S.	N.S.	0.006	0.009	N.S.
CI	0.001	0.001	0.004	N.S.	0.001	0.051	N.S.	N.S.	0.001	0.017	0.010
SJL	0.036	0.001	N.S.	N.S.	0.001	N.S.	N.S.	N.S.	0.001	0.001	N.S.
KC	0.048	0.001	N.S.	0.025	0.001	N.S.	0.019	N.S.	0.001	0.011	0.086
IP	0.004	0.001	N.S.	0.027	0.003	0.048	N.S.	N.S.	0.031	0.008	N.S.
DOF	0.009	0.001	0.008	N.S.	0.001	0.020	0.087	0.004	0.001	0.001	N.S.

Note: In all sites and treatments, PTA > PEE > PEU, except in SSC and DOF, where in the low treatment PEU > PEE. Int^1 . Interaction of that contrast with treatment. All significant interactions in the PEE *vs.* PTA by treatment were due to scale effects. In the case of PEE *vs.* PEU, interactions were due to rank changes.

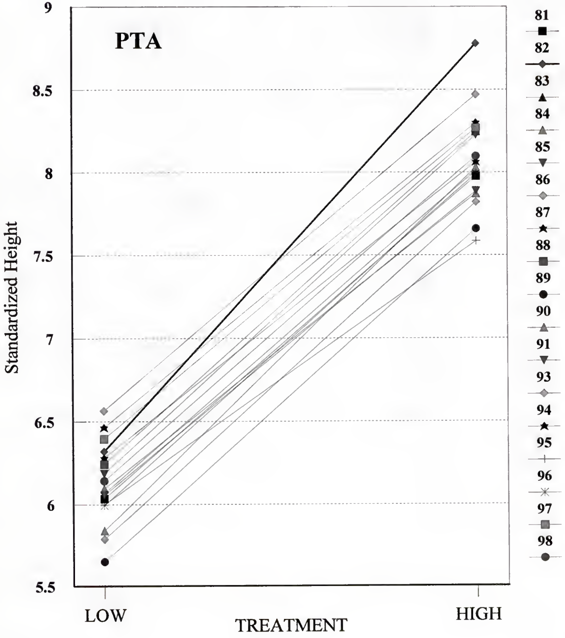
APPENDIX E
STANDARDIZED MEAN HEIGHT OF EACH **PEE** FAMILY IN EACH TREATMENT.

Type B genetic correlation for treatments ($r_{b\text{-treat}}$) was 0.74. Without the responsive family (57), $r_{b\text{-treat}}$ is equal to 0.94. Each point is the average across 10 sites.



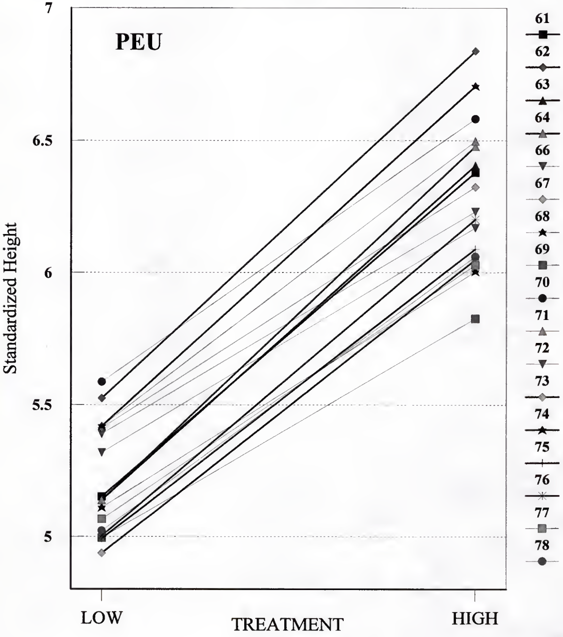
APPENDIX F
STANDARDIZED MEAN HEIGHT OF EACH **PTA** FAMILY IN EACH TREATMENT.

Type B genetic correlation for treatments ($r_{b\text{-treat}}$) was 0.74. Without the responsive family (82), $r_{b\text{-treat}}$ is equal to 0.94. Each point is the average across 10 sites.



APPENDIX G
STANDARDIZED MEAN HEIGHT OF EACH **PEU** FAMILY IN EACH TREATMENT.

Type B genetic correlation for treatments ($r_{b\text{-treat}}$) was 0.91. Two groups of families are differentiated as responsive (thicker line) and less responsive. Each point is the average across 10 sites.



APPENDIX H
INCIDENCE OF SLASH PINE CLONES USED TO CREATE THE HYBRIDS FAMILIES TESTED BY GROUP OF SERIES (SITES SHARING GROWERS)

SLASH (FEMALE) IN TEST	SITES BY SERIES / MALE											
	SSC - TC- GP				RAY - GFC				CI - PCA - SJL			
	F1H	PCH	PCB	PTA	F1H	PCH	PCB	PTA	F1H	PCH	PCB	PTA
1	x	x	x	x	x		x	x	x		x	x
2	x			x	x			x				x
3	x	x	x	x	x	x		x	x	x		x
4	x	x	x	x	x	x	x	x	x	x	x	x
5	x	x	x	x	x			x	x			x
6	x	x			x	x			x	x		
7	x	x	x	x	x		x	x	x		x	x
8												x
9		x	x			x	x			x	x	x
10		x	x			x	x			x	x	
11							x				x	
12							x				x	
13	x			x	x			x	x		x	x
14	x			x	x			x	x			x
15	x	x	x	x	x	x		x	x	x		x
17			x	x				x	x			x
18		x	x			x	x			x	x	
20	x	x	x	x	x	x		x	x	x		
21	x		x	x	x		x	x	x		x	x
22					x							x
23	x		x	x	x		x	x	x		x	x
24			x	x		x		x	x	x		x
25	x	x	x	x	x		x	x	x		x	x
26	x	x	x	x		x	x	x	x	x		
27		x										
28		x										
29		x										
30	x				x							

For PEExPCH and PEExPCB some family bulks were formed to completed 16 "families" in sites RAY, GFC, SJ, CI, and PCA. In parentheses is showed the clones that were included in each bulk. Thus, there were six family bulks for PEExPCH: 31 (13+14), 32 (21+22), 33 (7+27), 34 (23+25), 35 (16+28+30) and 36 (8+12+17); and five family bulks for PEExPCB: 41 (5+13+14+22), 42 (6+15), 43 (8+16+29+30), 44 (2+17), and 45 (24+26+27+28).

APPENDIX I

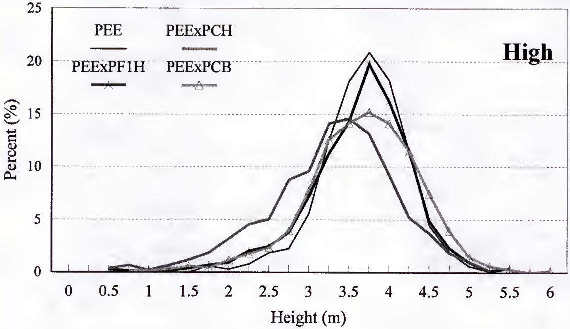
PERCENTAGES OF SURVIVAL AND MORTALITY DUE TO COLD, FUSIFORM RUST OR OTHER CAUSES AT THREE-YEARS OF AGE.

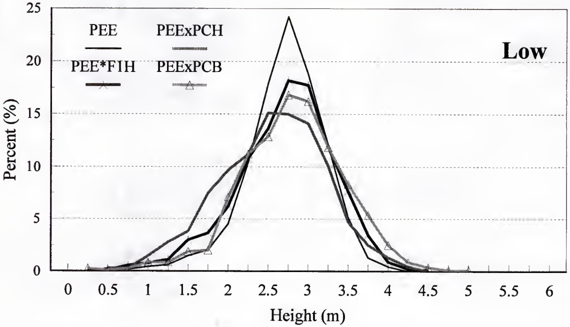
TAXON	Survival (%)	Mortality (%)		
		Cold	Rust	Other
PTA	97.4 (93 -100)	0.1 (0 -0.2)	0.4 (0 - 1.3)	2.1 (0.6 -6.5)
PEE x PTA	77.2 (71 - 84)	2.3 (0.2 - 5)	2.7 (0.2 - 6.4)	17.8 (9 -22.5)
PEE	95.1 (92 - 98)	0.4 (0 - 1.8)	0.7 (0 - 1.8)	3.8 (2.5-5.0)
PEE x F1H	89.1 (83 - 96)	1.4 (0.2 - 4)	2.9 (0.2- 4.6)	6.6 (3.1-13.8)
PEE x PCH	68.6 (49 - 83)	14.7 (0.2 -39)	4.3 (0 - 9.2)	12.4 (4.6-24.6)
PEE x PCB	89.1 (79 - 96)	1.3 (0.6 - 2)	4.5 (0.2 -9.0)	5.1 (1.7-10.4)

Values are across eight sites but in parentheses is the range at individual sites. For survival taxon differences were significant at $p<0.0001$, but for treatments non significant differences were found.

APPENDIX J
FREQUENCY POLYGON OF THIRD-YEAR HEIGHT FOR THE IMPROVED SLASH (PEE), AND THE PEE x F1H, PEE x PCH AND PEE x PCB HYBRIDS IN THE HIGH AND LOW TREATMENTS

Frequencies are for rust-free trees. Height values were adjusted as described in figure 4-5.





APPENDIX K
ANALYSIS OF THE COEFFICIENT OF VARIATION (CV) FOR THIRD-YEAR HEIGHT WITH RUST-FREE DATA

Source	CV -Height		
	DF	F value	Pr > F
SITE	6	1.97	N.S.
TREATMENT (H *vs.* L)	1	7.05	0.0348
SITE*TREATMENT	6	2.35	0.0068
TAXON	5	24.07	0.0001
[a]Hybrid Vigor in PEE x PTA	1	111.84	0.0001
[b]Hybrid Vigor in PEE x F1H	1	0.30	N.S.
PEE *vs.* PEE x PCH	1	12.87	0.0008
PEE *vs.* PEE x PCB	1	2.12	N.S.
PEE x PCH *vs.* PEE x PCB	1	4.14	0.0406
SITE*TAXON	30	2.51	0.0224
TREATMENT*TAXON	5	1.81	N.S.
SITE*TREAT*TAXON	30	1.89	N.S.
FAMILY(TAXON)	112	2.12	0.0008
SITE*FAMILY(TAXON)	479	1.03	N.S.
TREAT*FAMILY(TAXON)	111	1.14	N.S.
SITE*TREAT*FAMILY	416	1.13	0.0596
ERROR	1614		

Data were pooled across seven sites and two management levels.

a. Hybrid vigor of the PEE x PTA hybrid was analyzed by: PEE x PTA / (0.5 PEE + 0.5 PTA).

b. Hybrid vigor of the PEE x F1H backcross hybrid was analyzed by: PEE x F1H / (0.5 PEE + 0.5 PEE x PCH).

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BIOGRAPHICAL SKETCH

Javier López Upton was born in Puebla City, México, on August 6, 1963, to Fernando López Mascarúa and Blanca Rosa Upton Fayos. After a happy life in Monterrey and Puebla cities during his elementary studies, he started a bachelor's degree at the Universidad Autónoma Chapingo, where he graduated in 1985. He began working in the Programa Forestal of the Colegio de Postgraduados en Ciencia Agrícolas (C.P.). Then he started a master degree in forestry in the C.P. After graduation in 1990, he returned to the C.P. to become adjunct researcher, and later staff researcher. Then, in order to escape poverty, he decided to married Ma. Eugenia Peña Ortega in 1992. After completing too many requirements, including the TOEFL and GRE examinations and all the paperwork, he received a scholarship to become a graduate student at the University of.Florida in 1995.

Most importantly he become a father when Blanquita was born in 1994, and when Adris was born in 1995. Now, although he still has a low salary, he is happily working and eating true Mexican food in México “Lindo” and “Querido”.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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